S. P. WILTSHIRE.

VOL. XX, PART II Published 30 January 1936

The British Mycological Society

(*Recognosce notum, ignotum inspice*)

TRANSACTIONS

Edited by

J. RAMSBOTTOM, B. F. BARNES and H. WORMALD

Price to non-members, Seven Shillings & Sixpence

LONDON
CAMBRIDGE UNIVERSITY PRESS
FETTER LANE, E.C. 4
CHICAGO: THE UNIVERSITY OF CHICAGO PRESS
(AGENTS FOR THE UNITED STATES)
BOMBAY, CALCUTTA, MADRAS: MACMILLAN
TOKYO: MARUZEN COMPANY LTD.

All rights reserved

PRINTED IN GREAT BRITAIN

LIST OF OFFICERS AND COUNCIL FOR 1935

Elected September 1934

President

Dr MALCOLM WILSON, D.Sc., F.R.S.E., F.L.S.

Vice-Presidents

Dr B. BARNES, D.Sc., PH.D., F.L.S.

F. G. GOULD.

General Secretary

J. RAMSBOTTOM, O.B.E., M.A., Sec.L.S.

British Museum (Nat. Hist.), Cromwell Road, London, S.W. 7.

Secretary

Miss E. M. WAKEFIELD, M.A., F.L.S.

The Herbarium, Royal Botanic Gardens, Kew, Surrey.

Treasurer

A. A. PEARSON, F.L.S.

59 Southwark Street, London, S.E. 1.

Editors

J. RAMSBOTTOM, Dr B. BARNES

and

Dr H. WORMALD.

COUNCIL

The OFFICERS, with the following in addition:

A. W. BARTLETT, F. T. BROOKS, Prof. W. BROWN, Prof. A. H. R. BULLER, Dr E. J. BUTLER, E. N. CARROTHERS, K. ST G. CARTWRIGHT, C. G. C. CHESTERS, A. D. COTTON, Dame H. C. I. GWYNNE-VAUGHAN, H. J. HOWARD, H. H. KNIGHT, Dr G. H. PETHYBRIDGE, Prof. M. C. POTTER, C. REA, Prof. E. S. SALMON, E. W. SWANTON.

COMMITTEE FOR PLANT PATHOLOGY

Prof. W. B. BRIERLEY	L. OGILVIE
W. BUDDIN (*Secretary*)	Dr G. H. PETHYBRIDGE (*Chairman*)
K. ST G. CARTWRIGHT	Miss K. SAMPSON
Dr W. J. DOWSON	Dr W. M. WARE
W. C. MOORE	S. P. WILTSHIRE
A. E. MUSKETT	Dr H. WORMALD

THE PRESIDENT and SECRETARIES of the Society *ex officio*

The subscription price is £1. 10*s*. per volume (post-free), payable in advance; single numbers 7*s*. 6*d*. net (double numbers 15*s*. net). Subscriptions may be sent to any Bookseller, or to the Cambridge University Press, Fetter Lane, London, E.C. 4.

The Cambridge University Press has appointed the University of Chicago Press agents for the sale of *The British Mycological Society's Transactions* in the United States of America.

NOTES ON CERTAIN CHANGES IN NOMENCLATURE IN THE SECOND EDITION OF THE LIST OF COMMON NAMES OF BRITISH PLANT DISEASES

By E. M. WAKEFIELD and W. C. MOORE

A standardised "List of common names of British plant diseases" was published in the Society's *Transactions* in 1929 (xiv (1929), 140–77). Recently this list has been revised* and now contains the names of seven additional hosts and some fifty additional diseases.

In this second edition of the list only a few changes have been made in the common names of the diseases, but considerable revision of the scientific names of the relevant pathogens has been found necessary both to bring matters into line with more recent research and in order to ensure conformity to the International Rules of Botanical Nomenclature as revised at Cambridge in 1930. The present article provides explanations for most of the nomenclatorial changes found necessary, and the notes are arranged in groups corresponding to the main groups under which the host plants are arranged in the list. It may be mentioned here, however, that in naming species of *Fusarium* Wollenweber's(68) classification has been followed throughout. On the other hand, since the classification and nomenclature of bacteria is at present under consideration by the International Society for Microbiology, no attempt has been made to adhere strictly to any one system of bacterial nomenclature, and the names commonly used in this country have been adopted in all instances. Many of the additions denote diseases that were not known to occur in this country at the time the list was originally prepared. Certain other diseases have now been included on account of their increased prevalence during recent years or because the host involved has come more into prominence commercially.

Cereals

The name *Ustilago Hordei* was used for Covered Smut of barley by Lagerheim(37) in 1889, and since Kellerman and Swingle(35) did not use this combination until the following year, (Pers.) Lagerh. and not (Pers.) Kellerm. & Sw. must be cited as the authority for the name.

Ustilago Tritici presents a similar but rather more difficult case. In

* It has been published as a separate pamphlet and is obtainable from the University Press, Cambridge.

the *Second Annual Report for* 1889 *of the Kansas Experimental Station*, appearing in 1890, Kellerman and Swingle ((35), p. 261) first published the name *U. Tritici* (Pers.) Jens., on the basis of information given in a letter received from Jensen and dated January 24th, 1890. This combination has been quoted by most later authors and was adopted in the first edition of the list. As pointed out by Liro(40), however, the same combination was also made by Rostrup(58) on March 31st of the same year. The *Kansas Report* for 1889 bears only the date 1890, but in the Report of the Council given in the *Kansas Third Annual Report for* 1890 (1891), pp. vii–xii, it is stated that "the second annual report (1889)... was issued from the press of the Kansas Publishing House in June". Rostrup's article therefore antedates that of Kellerman and Swingle, and for this reason the name *U. Tritici* (Pers.) Rostr. is now cited.

The double citation, (Bri. & Cav.) Eid., used for *Helminthosporium Avenae* in the first edition was a mistake which appears to have originated in a paper by Ravn(56) and was not detected at the time the list was prepared. This fungus was originally named as var. *Avenae-sativae* of *Helminthosporium teres* by Briosi and Cavara(8). When Eidam(23) raised it to the rank of species he used the epithet *Avenae*, and not *Avenae-sativae*. Article 58 of the Rules states that when the rank of a group is changed the earliest legitimate name or epithet given to the group in its new rank is valid, provided it is not a later homonym. Accordingly the correct name for the fungus as a species is *Helminthosporium Avenae* Eid., and this cannot be discarded in favour of *H. Avenae-sativae* (Bri. & Cav.) as was done by Lindau (1910, in *Rab. Krypt.-Fl.* ed. 2, Bd. 1, Abt. 9, p. 35). Ravn's use of (Bri. & Cav.) in parenthesis for the epithet *Avenae* was either a *lapsus calami* or due to a misunderstanding of the significance of brackets in citations of authors' names. Both *Pyrenophora Avenae* Ito and *Pleospora Avenae* Schaffn. & Rathschl. have been described as the perfect stage of *Helminthosporium Avenae*, and the first named has recently been recorded in Britain by Dennis(18).

Diedicke(19), in 1903, merely surmised the existence of a "*Pleospora teres*" on barley; he did not see it. Hence his combination is not valid, and Drechsler's(22) *Pyrenophora teres* is the first legitimate name given to the perfect stage. The correct citation is therefore *P. teres* Drechsl. and not *P. teres* (Died.) Drechsl. as previously given.

A disease of oats occurring in Wales and previously believed to correspond to Halo Blight (*Bacterium coronafaciens* Ch. Elliott) has now been shown by Davies and Jones(16) to be identical with the non-parasitic Grey-Leaf. There is no evidence that true Halo Blight occurs in Britain, and the entry has therefore been deleted.

PULSE

Further studies of Chocolate Spot of broad beans have made it doubtful whether this disease is caused by *Bacillus Lathyri* Manns & Taubenh. Riker and Riker(57) suggest that a bacterium closely resembling *Pseudomonas seminum* Cayley might be involved, whilst unpublished work carried out at Cambridge appears to show that the disease may be due to a fungus. Hence the insertion of a (?) before the name *Bacillus Lathyri* under broad beans and also under sainfoin, vetches and sweet pea. On the other hand, the evidence that Marsh Spot of peas is not a parasitic disease is now very strong (9, 36, 52): it is therefore classed as non-parasitic.

Until recently all the damage to pea plants associated with *Ascochyta* in this country has been attributed to *A. Pisi*. It is now known that the three diseases, caused by three distinct species of *Ascochyta*, and first differentiated in America independently by Linford and Sprague(39) and by L. K. Jones(33), all exist in Britain, although their relative importance has not yet been determined. The true *A. Pisi* Lib. produces leaf, stem and pod spotting only, and the name suggested for the disease it causes is Leaf and Pod Spot. The other two species (*Mycosphaerella pinodes* (Berk. & Blox.) Stone* and *Ascochyta pinodella* L. K. Jones) affect the plant in much the same way, but, in addition, they may attack the base of the stem, inducing a Foot Rot. These two species, together with species of *Fusarium* frequently associated with a stem rot of pea occurring in the west of England(48), are grouped together as the pathogens of a disease to which the name Foot Rot has been applied.

In the first edition Root Rot of peas was ascribed to *Aphanomyces euteiches* Drechsl. and to *Thielavia basicola* Zopf. In 1912 Ferraris(24) applied the name *Thielaviopsis basicola* to what was considered to be the imperfect stage of the last-named fungus, in order to distinguish it from the ascospore stage. He did not, however, imply the existence of two distinct fungi. In 1925 McCormick(43) brought forward evidence, based on cultural work, which strongly suggested that *Thielavia basicola* and *Thielaviopsis basicola* are not genetically connected, although often associated with one another. Since it is the conidial stage that is commonly found associated with rotting of pea roots in Britain the name *Thielaviopsis basicola* (Berk. & Br.) Ferraris has been selected in preference to *Thielavia basicola* Zopf, and the opportunity has been taken to distinguish Black Root Rot due to this fungus from Root Rot due to *Aphanomyces*.

* The name Niessl was left in the list by an oversight. Niessl called the fungus *Sphaerella*. The change to *Mycosphaerella* was made by Stone (*Ann. mycol.* x (1912), 581).

Potato

The only significant emendation made in the section dealing with potato diseases is that relating to Spraing. Brown spotting or streaking of the flesh of potato tubers, quite distinct from the brown decay due to blight, has been known in Britain for over half a century, but its true nature and origin have always been, and still are, a matter of considerable uncertainty. In England the malady was at first called Canker or Internal Disease, but later the Scottish term Sprain or Spraing came into more general use, both in this country and in Ireland. Horne (31) clearly distinguished two diseases in this category and called them Blotch or Internal Disease, and Sprain or Streak Disease. In Blotch, larger or smaller, brown or chocolate specks, spots or blotches were distributed throughout the flesh of the tubers, whilst in Sprain the markings were usually arc-like or curved in section and often arranged concentrically. Later, Paine (49) introduced the name Internal Rust Spot to include both these sets of symptoms; and they remained grouped together until quite recently, when Grieve (26) segregated them again. In the present list the name Spraing is retained for the disease exhibiting arc-like lesions and the term Internal Rust Spot is applied to the blotch type of lesion. It should be noted, however, that these two types of lesion occasionally occur together in the same tuber. There is at present no evidence that the allied diseases Pseudonetnecrosis and Net Necrosis occur in this country. Spraing has been attributed by different workers to non-parasitic causes (25), to bacteria (10) and to virus agency (26, 55), and the last-mentioned is adopted provisionally in the list. There is some evidence that Internal Rust Spot may be bacterial in nature (10, 26, 49), but the matter has not yet been satisfactorily elucidated.

Root crops

Opinions differ as to the appropriateness of the names Finger-and-Toe and Club Root for the disease of Crucifers caused by *Plasmodiophora Brassicae*. In this country usage is about equally divided between them, but in parts of the Empire (15) Club Root appears to be preferred, and largely on account of this the name Finger-and-Toe has now been replaced by Club Root as a common name under turnip, cabbage, radish, seakale and wallflower.

In the first edition Soft Rot of turnip and swede was ascribed to two distinct organisms, *Bacillus carotovorus* L. R. Jones and *Pseudomonas destructans* Potter. The original cultures from which Potter (53) described his organism as a uniflagellate rod were lost, but two later isolations by Potter, which he believed to be identical with his original isolation, were found by Harding and Morse (28) to consist of an organism with peritrichiate flagella which they regarded as

specifically identical with *Bacillus carotovorus*. Since Potter(54) himself appears to have accepted this interpretation the disease is now attributed to *B. carotovorus* only.

White Spot of turnip, previously ascribed to *Cercospora Bloxami* Berk. & Br., is now attributed to *Cercosporella Brassicae* (Fautr. & Roum.) v. Hoehn.*

Vegetables

For many years the Downy Mildew of onions and of shallots has been known as *Peronospora Schleideni* Unger, and this was the name included in the first edition of the list. In 1932, however, Cook(13) endeavoured to prove that it should be called *P. destructor* (Berk.) Caspary. Unfortunately Article 57 of the International Rules, concerning the names of fungi having a pleomorphic life cycle, does not mention the Phycomycetes. Mycologists, however, appear to be agreed that the rule should apply to this group also, and it is therefore necessary to discover the name first given to the "perfect" or oospore stage.

The conidial stage of the onion Downy Mildew was first described by Berkeley(6), in 1841, as *Botrytis destructor* Berk., but later, in 1860(7), he listed it as *Peronospora destructor* Casp. Unger's name *P. Schleideni* dates from 1847(66), and similarly applies only to the conidial stage. In 1855 Caspary(11) described oospores of various species of *Peronospora*, but there seems to be no evidence that he ever saw those of the onion fungus, and he himself does not appear to have published the combination *P. destructor*. Cook(13) maintained that because Berkeley used this name for his fungus, and mentioned in the generic description of *Peronospora* that the genus produces oospores, therefore the name *P. destructor* was applied to the perfect stage. The argument is false, however, and it cannot be assumed that Berkeley received a private communication from Caspary stating that he had seen oospores. It seems much more probable that Berkeley merely followed Caspary in including this species in the genus *Peronospora* on general grounds. In point of fact, three years after publication of the name *P. destructor* by Berkeley, de Bary(17) wrote of the onion fungus "oosporis ignotis".

As far as can be ascertained the oospores of onion Downy Mildew were first mentioned by W. G. Smith(62) in 1884. He gave an illustration of them and stated that they had been found by Vize in decaying patches on onions that had previously borne the conidial stage. Shipley(61) fully described the oospores, and his illustrations of them were drawn by W. G. Smith. In both instances the name used was *P. Schleideniana*, a combination made by de Bary(17) in 1863. De Bary's name was nevertheless invalid, for he merely applied it instead

* See p. 110.

of *P. Schleideni* to the conidial stage, and names cannot be changed arbitrarily. Since W. G. Smith used this combination for the oospore stage, however, it is correct to call the fungus *P. Schleideniana*, but the name must be attributed to W. G. Smith and not to de Bary.

The laws of priority necessitated the change from *Colletotrichum oligochaetum* Cav. to *C. lagenarium* (Passer.) Ell. & Hals. for the fungus causing Anthracnose of cucumber. This organism was first described in 1867 by Passerini (50) as *Fusarium lagenarium*, and it was transferred, first to *Gloeosporium* and later, in 1893, by Halsted (27) to *Colletotrichum* as *C. lagenarium* Ell. & Hals. Meanwhile, in 1889, Cavara (12) had described what is now regarded as the same species, as *C. oligochaetum* and his name is commonly but incorrectly given to the fungus.

The organism causing Bacterial Spot of lettuce is *Bacterium marginale* N. A. Brown and, adopting a suggestion by Prof. S. G. Paine, this name is no longer given as a synonym of *B. pyocyaneum* (Gessard) Lehm. & Neum. (45). Paine has pointed out (*in litt.*) that when first isolated from affected lettuce *B. marginale* does not exhibit the deep green colour of *B. pyocyaneum*; moreover, the last-named is regarded by medical workers as a human pathogen and, until further information is forthcoming, it is desirable to avoid possible exaggeration of the importance of this organism in comparative animal and plant pathology.

The authority for the name *Marssonina panattoniana* Berl. is now correctly given as (Berl.) Magn. In 1906 Magnus (42) showed that the name *Marssonia* (often wrongly spelt *Marsonia*) was given by Karsten to a Phanerogamic genus in 1861, thirteen years before Fischer chanced upon the same name to designate a fungus. Fischer's name was therefore an invalid one and Magnus replaced it by *Marssonina*, to which he transferred various species, including *M. panattoniana* Berl. The use of brackets for Berl., the first author of the epithet *panattoniana*, is, of course, in accordance with Article 49 of the International Rules, which lays down that when a species is either transferred to another genus, or altered in rank, but *without changing its specific epithet*, the name of the original author must be cited in parenthesis.

Recent investigations (3) have permitted more precise definition to be made of the virus diseases of tomato, and Spotted Wilt, Mosaic, Yellow Mosaic and Streak are now differentiated. In the past the last-named has often been called Stripe, but it is considered desirable to reserve the name Stripe for the disease ascribed to *Bacillus Lathyri* Manns & Taubenh. The term Streak as now applied embraces four distinct Streak diseases caused by different viruses but indistinguishable by their symptoms alone. Only two of these, viz. Single-virus Streak and Mixed-virus Streak, are known to occur in this country.

The common name for the disease of cabbage due to *Phoma*

Lingam (Tode) Desm. has been changed from Stem Rot to Canker to meet a criticism made by Cunningham (15).

Fruit

Changes have been made in the name and authorities of the two Brown Rot fungi *Sclerotinia fructigena* Schroet. and *S. cinerea* Schroet. wherever they occur in the list. In 1893, Schröter (59), who contributed the section on fungi to Cohn's *Kryptogamen-Flora*, discussed the two species *Monilia fructigena* and *M. cinerea* and named them *Sclerotinia fructigena* and *S. cinerea* respectively. Reference to his descriptions, however, shows clearly that he did so only by analogy, for he stated that the perfect stages of these fungi had not been found. His combinations are therefore invalid.

As pointed out by Harrison (29), the first description of the perfect stage of *Monilia fructigena* appears to be one by Aderhold and Ruhland (2) in 1905, and the correct citation for the common fruit-rotting fungus of Europe having buff-coloured fructifications is therefore *Sclerotinia fructigena* Aderh. & Ruhl.

In the same article Aderhold and Ruhland described two other fungi in their perfect stages, viz. *Sclerotinia laxa* and *S. cinerea*. The account of *S. laxa* was based upon European material, and this would appear to be the first description of the perfect stage of what has long been known in Europe as *Monilia cinerea* Bon. The strains of this fungus that cause Brown Rot, Blossom Wilt and allied diseases of pear, plum, cherry, apricot and peach all appear to be identical, and they should all be included under the name *Sclerotinia laxa* Aderh. & Ruhl. The strain that causes Brown Rot and Blossom Wilt of apple is apparently a distinct biologic form, known hitherto as *S. cinerea* f. *Mali*, but now correctly named *S. laxa* Aderh. & Ruhl. f. *Mali* (Worm.) Harrison (29).

Aderhold and Ruhland's description of *S. cinerea*, on the other hand, was based on material received from America, and these authors were mistaken in assuming that they were dealing with the perfect stage of the European *Monilia cinerea* Bon. In point of fact they had before them a specimen of the common American Brown Rot fungus, now generally called *Sclerotinia fructicola* (Wint.) Rehm, which is unknown in this country. Indeed, it is very doubtful whether it occurs normally in Europe, although it was isolated once some years ago in Holland from an apple fruit.

Cooke (14), in 1866, first described the ascigerous stage of the Apple Scab fungus as *Sphaerella inaequalis*. The combination *Venturia inaequalis*, usually attributed to Aderhold (1), was actually made by Winter much earlier and was used in Thuemen's *Mycotheca Universalis*, Nos. 261, 650 and 1544, issued 1875, 1877 and 1880 respectively. The name was used by Winter in a rather wider sense than it is now,

but that does not affect its validity, and the correct citation is *V. inaequalis* (Cooke) Wint. For precision "emend. Aderh." may be added, since the type of Cooke's *Sphaerella inaequalis* was a form on *Pyrus Aria* and not on apple.

With regard to the species of *Myxosporium* causing Surface Canker of apple, since the mistake is so often made it seems desirable to point out that the specific epithet should be *corticola* and not "*corticolum*", as was wrongly used by Edgerton. Latin words ending in *-cola*, as *incola*, *agricola*, *terricola*, are not adjectives, but nouns of common gender, formed from the stem *col*. There is no corresponding adjectival form. The specific epithet *corticola* is thus a noun in apposition, meaning an inhabitant of the bark; it cannot be declined like an adjective. The perfect stage of this fungus has not yet been found in this country, but it is known on the Continent under three different names. Madame Arnaud (4) first described it in France in 1923 as *Dermatea corticola* Arn. In 1930 Jørgensen (34) encountered what is clearly the same organism in Denmark, but he was apparently unaware of Arnaud's work and regarded his fungus as new to science, naming it *Neofabraea corticola*. More recently Nannfeldt (47) has considered the genus *Neofabraea* to be synonymous with *Pezicula*, and has called the apple fungus *Pezicula corticola* (Jørgens.) Nannf. The correct double citation under *Pezicula*, if the synonymy is correct, should be *P. corticola* (Arn.) Nannf.

Physalospora obtusa (Schw.) Cooke has been substituted for *P. Cydoniae* Arn. as one of the causal agents of Leaf Spot of apple, in accordance with recent investigations by Stevens (63), and similarly *Plectodiscella veneta* Burkh. has been replaced by *Elsinoe veneta* (Burkh.) Jenk. for Anthracnose of raspberry (32), while *Gloeosporium ampelophagum* (Pass.) Sacc. has been listed as a synonym of *Elsinoe ampelina* Shear for Anthracnose of grape vine (60). As regards Rust of black currants, *Cronartium ribicola*, Sydow (64) has submitted legitimate reasons for citing J. C. Fischer instead of Diet. as the authority for the name.

Loganberry Rust and Branch Die Back of plums have been deleted from the list on account of their apparent rarity in this country. Rough Scab of apples has also been omitted, since in view of recent research by Moore (46) it is very doubtful whether this name can be applied to any specific disease, or whether the fungus to which it was attributed (*Coniothecium chomatosporum* Corda) can be regarded as actively parasitic. On the other hand, there are now more cogent reasons for regarding the Sooty Blotch fungus on apples in this country as identical with *Gloeodes pomigena* (Schw.) Colby, and a correction to this effect has been made.

Recent investigations have helped considerably to elucidate the obscurity regarding Die Back in plum trees. Bacteria were pre-

viously thought to be implicated, and Wormald's work (69) has now revealed the existence of a specific disease caused by *Pseudomonas mors-prunorum* Worm. This disease has therefore been removed from the congeries of undetermined diseases included under the term Die-Back and has been named Bacterial Canker.

Ornamentals

The only change made in the common names under this section is the replacement of the name Stalk Break by the more appropriate term Loose Bud for a non-parasitic condition not infrequently exhibited by hyacinths (51).

The discovery and naming of the perfect stage of the gladiolus Dry Rot organism, *Sclerotium Gladioli* Massey, enables attention to be drawn to a further point in nomenclature often unappreciated by plant pathologists. In fungi with a pleomorphic life cycle, the name to be used is the earliest given to the state which it has been agreed to call the perfect form, provided that this name is otherwise in accordance with the International Rules (Art. 57). It frequently, indeed usually, happens that the author describing the perfect stage uses the same specific epithet as that of the conidial or sterile form previously known. Many writers cite the name of the author of the conidial stage in parenthesis. For instance, when Drayton (21) found that *Sclerotium Gladioli* Massey produces a *Sclerotinia* as the perfect state he wrote its name *Sclerotinia Gladioli* (Massey) Drayton. Since the *Sclerotinia* was a fungus described *de novo*, however, and it was not merely a question of changing an existing name which already had a full description, the case is not quite the same as that provided for in Art. 49. If the ascigerous stage had previously been described as *Peziza* by Massey, the double citation (Massey) Drayt. would have been correct. The two cases are not parallel, and for this reason the brackets have been omitted here and in all instances where it is known that the first author described only the conidial or imperfect stage.

Phytophthora Richardiae Buism., the causal agent of Root Rot of arum (*Richardia*), is considered by Ashby (5) to be merely a variety of *P. cryptogea* and it is now listed as *P. cryptogea* Pethybr. & Laff. var. *Richardiae* (Buism.) Ashby.

As shown by Wollenweber ((68), p. 499) the carnation Leaf Rot fungus described by Höstermann and Laubert in 1921 as *Pseudodiscosia Dianthi* is identical with *Excipulina valtellinensis* Trav. (1903). This fungus is, however, a *Heteropatella* and its correct name is *H. valtellinensis* (Trav.) Wr.

A description of the species of *Penicillium* that causes Storage Rot of gladiolus was published from two sources early in 1928, and in both instances the name *P. Gladioli* was used. A preliminary account

of it was published by McCulloch and Thom(44) in No. 1730 of *Science*, issued on February 24th, 1928, and these authors were cited as the authorities for the name in the first edition. Machacek(41), however, described the same fungus under the same name in the *19th Ann. Rep. Quebec Soc. Prot. Plants for* 1926–7, Quebec, 1927, p. 77, and, in 1930, Thom(65) ascribed priority of publication to Machacek. This view was adopted in the second edition, but subsequently it was discovered that according to Drayton(20) the publication containing Machacek's description was not distributed until February 28th, 1928. The correct authority for the name is therefore McCull. & Thom, as given in the first edition.

Although no change has been made in the name *Botrytis Tulipae* for Fire of tulips, enquiries have been received from time to time as to the reason for citing (Lib.) Lind as the authority instead of (Lib.) Hopk. It may be pointed out, therefore, that when Hopkins(30) made the combination in 1921 he overlooked the fact that Lind(38) had already used the same combination eight years previously.

Under iris Soft Rot *Bacillus omnivorus* van Hall has been listed as a synonym of *B. carotovorus* L. R. Jones in accordance with modern opinion, and delphinium Mildew, previously listed in error as *Erysiphe Cichoracearum* DC., has been correctly named *E. Polygoni* DC.

Recent unpublished work* in this country has demonstrated that Wilt of carnations, as previously understood, is not a single specific disease due to certain species of *Fusarium* but is a mixture of two or three distinct diseases. One of these—and perhaps the least important economically—has been differentiated as Die-Back (*Fusarium culmorum* (W. G. Sm.) Sacc.). The others are grouped together for the time being under the common name Wilt and Stem Rot, attributed to species of *Verticillium* and *Fusarium*.

In view of Waterman's(67) conclusions that *Coniothyrium Fuckelii* Sacc. and *C. Rosarum* Cooke & Harkn. are identical it was decided to omit Graft Disease as a rose disease distinct from Stem Canker. Since the perfect stage of the fungus has been found in this country Stem Canker is now attributed to *Leptosphaeria Coniothyrium* (Fuck.) Sacc. The so-called Brand Canker, due to *Coniothyrium Wernsdorffiae* Laub., has not yet been found in England.

In the first edition Leaf Spot of viola and violet was attributed in part to *Ascochyta Violae* Sacc. & Speg. From examination of typical specimens during the past few years, however, it would appear that the fungus commonly causing Leaf Spot of violets in this country does not correspond to the original description of *A. Violae* Sacc. & Speg. It not infrequently produces two-celled spores and is therefore perhaps correctly to be regarded as a species of *Ascochyta*, but

* For a brief reference to the results of this research see *The Fruit Grower*, LXXVII (1934), 179.

in general it seems to agree closely with the description of *Phyllosticta Violae* Desm., and it is provisionally referred to that species. As a cause of Leaf Spot in violas and pansies *P. Violae* appears to be uncommon in England, and this entry has accordingly been deleted.

Miscellaneous

Thielavia basicola Zopf is renamed *Thielaviopsis basicola* (Berk.) Ferraris (see p. 99) under Root Rot of tobacco, and a short list of fungi known to attack lawn grasses in this country has been added. Little attention has hitherto been paid to turf diseases, and for the present no useful purpose would be served by attempting to apply common names to them.

REFERENCES

(1) Aderhold, R. "Revision der Species *Venturia chlorospora*, *inaequalis* und *ditricha* autorum." *Hedwigia*, xxxvi (1897), 67.

(2) Aderhold, R. and Ruhland, W. "Zur Kenntnis der Obstbaum-Sklerotinien. *Arb. biol. Abt.* (*Land.-u. Forstwirts*), Berl., iv (1905), 427–42.

(3) Ainsworth, G. C., Berkeley, G. H. and Caldwell, J. "A comparison of English and Canadian tomato virus diseases." *Ann. appl. Biol.* xxi (1934), 566–80.

(4) Arnaud, Mme. "Sur un champignon parasite des branches du Poirier: le *Dermatea corticola* n.sp." *Rev. Path. vég.* x (1923), 303–7.

(5) Ashby, S. F. "Further note on the production of sexual organs in paired cultures of species and strains of *Phytophthora*." *Trans. Brit. mycol. Soc.* xiv (1929), 259.

(6) Berkeley, M. J. "Notices of British fungi." *Ann. Mag. nat. Hist.* vi (1841), 436.

(7) —— *Outlines of British Fungology* (1860), p. 349. London.

(8) Briosi, G. and Cavara, F. *I funghi parassiti delle piante coltivate od utili*, No. 80 (1889). Pavia.

(9) Bruijn, H. L. G. de. "Kwade harten van de erwten." *Tijdschr. PlZiekt.* xxxix (1933), 281–318.

(10) Burr, S. "Sprain or Internal Rust Spot of potato." *Ann. appl. Biol.* xv (1928), 563–85. See also xviii (1931), 521–23.

(11) Caspary, R. "Über einige Hyphomyceten mit zwei- und dreierlei Früchten." *Monatsber. Kgl. Preuss. Akad. Wiss. Berlin* (1855), pp. 308–33.

(12) Cavara, F. "Matériaux de mycologie lombarde." *Rev. mycol.* xi (1889), 191.

(13) Cook, H. T. "Studies on the Downy Mildew of onions, and the causal organism *Peronospora destructor* (Berk.) Caspary." *Mem. Cornell agric. Exp. Sta.* cxliii (1932), 40 pp.

(14) Cooke, M. C. "Foliicolous Sphaeriae." *J. Bot.* iv (1866), 248.

(15) Cunningham, G. H. "Standardisation of common names of plant diseases." *Trans. Brit. mycol. Soc.* xvi (1931), 145–8.

(16) Davies, D. W. and Jones, E. T. "Grey Speck disease of oats." *Welsh J. Agric.* vii (1931), 349–58.

(17) de Bary, A. "Recherches sur le développement de quelques champignons parasites." *Ann. Sci. nat.* (*Bot.*), Ser. 4, xx (1863), 122.

(18) Dennis, R. W. G. "Notes on the occurrence of *Pyrenophora Avenae* Ito in Scotland." *Trans. Brit. mycol. Soc.* xix (1935), 288–90.

(19) Diedicke, H. "Über den Zusammenhang zwischen *Pleospora*- und *Helminthosporium*-Arten II." *Z. Bakt.* Abt. ii, xi (1903), 56.

(20) Drayton, F. L. In "Report Dominion Botanist for 1927". *Rep. Dep. Agric. Can.* (*Bot.*) (1928), p. 28.
(21) —— "The gladiolus dry rot caused by *Sclerotinia Gladioli* (Massey) n.comb." *Phytopathology*, xxiv (1934), 397–404.
(22) Drechsler, C. "Some graminicolous species of *Helminthosporium*. I." *J. agric. Res.* xxiv (1923), 656.
(23) Eidam, E. "Das Vorkommen der Fleckenkrankheit auf Gersten- und auf Haferblättern." *Der Landwirt*, xxvii (1891), 509.
(24) Ferraris, T. "Hyphales." *Soc. Bot. Ital. Flora. Ital. Crypt.* i (1912), 233.
(25) Findlay, A. *The potato: its history and culture with descriptive list of varieties raised and introduced* (1905), pp. 6–8. Cupar, Fife.
(26) Grieve, B. J. "Studies in bacteriosis. XX. The Spraing disease of potato tubers." *Ann. appl. Biol.* xxi (1934), 233–50.
(27) Halsted, B. D. "Identity of anthracnose of the bean and watermelon." *Bull. Torrey Bot. Cl.* xx (1893), 246–50. See also *Rep. N.J. agric. Exp. Sta.* (*Bot.*) (1893), pp. 347–52.
(28) Harding, H. A. and Morse, W. J. "The bacterial soft rots of certain vegetables. I. Part i. The mutual relationships of the causal organisms." *Tech. Bull. N.Y. Sta. agric. Exp. Sta.* xi (1909), 256.
(29) Harrison, T. H. "Brown Rot of fruits and associated diseases of deciduous fruit trees. i. Historical review, and critical remarks concerning taxonomy and nomenclature of the causal organisms." *J. roy. Soc. N.S.W.* lxvii (1933), 132–77.
(30) Hopkins, E. F. "The *Botrytis* blight of tulips." *Mem. Cornell agric. Exp. Sta.* xlv (1921), 331.
(31) Horne, A. S. "The symptoms of internal disease and sprain (streak-disease) in potato." *J. agric. Sci.* iii (1910), 322–32. See also *Ann. appl. Biol.* i (1914), 194–6.
(32) Jenkins, A. E. "Elsinoe on apple and pear." *J. agric. Res.* xliv (1932), 696.
(33) Jones, L. K. "Studies of the nature and control of blight, leaf and pod spot, and footrot of peas caused by species of *Ascochyta*." *Bull. N.Y. St. agric. Exp. Sta.* No. 547 (1927), 46 pp.
(34) Jørgensen, C. A. "Barkkraeft paa Aeble og Paere, foraarsaget af *Neofabraea corticola* (Edgert.) C.A.J. n.sp. et n.comb." *Tidsskr. Planteavl*, xxxvi (1930), 800–11. See also *Bot. Tidsskr.* xli (1930), 227–39.
(35) Kellerman, W. A. and Swingle, W. T. "Report of the botanical department." *Rep. Kans. agric. Exp. Sta. for* 1889 (1890), pp. 213–88.
(36) Lacey, M. A. "Studies in bacteriosis. XXI. An investigation of Marsh Spot of peas." *Ann. appl. Biol.* xxi (1934), 621–36.
(37) Lagerheim, G. von. "Revision der im Exsiccat 'Kryptogamen Badens von Jack, Leiner und Stizenberger' enthaltenen Chytridiaceen, Peronosporeen, Ustilagineen und Uredineen." *Mitt. bad. bot. Ver.* (1889), p. 70.
(38) Lind, J. *Danish Fungi* (1913) (in Errata following p. 648). Copenhagen.
(39) Linford, M. B. and Sprague, R. "Species of *Ascochyta* parasitic on the pea." *Phytopathology*, xvii (1927), 381–97.
(40) Liro, J. I. *Die Ustilagineen Finnlands* (1924), p. 111. Helsinki.
(41) Machacek, J. E. "A *Penicillium* rot of gladiolus." *Rep. Quebec Soc. Prot. Pl.* 1926–7 (1928), pp. 77–86.
(42) Magnus, P. "Notwendige Umänderung des Namens der Pilzgattung *Marssonia* Fischer." *Hedwigia*, xlv (1906), 88–91.
(43) McCormick, F. A. "Perithecia of *Thielavia basicola* Zopf in culture and the stimulation of their production by extracts from other fungi." *Rep. Conn. agric. Exp. Sta.* (Bull. No. 269) (1925), pp. 539–54.
(44) McCulloch, L. and Thom, C. "A corm rot of gladiolus caused by a *Penicillium*." *Science*, lxvii (1928), 216–17.
(45) Mehta, M. M. and Berridge, E. M. "*B. pyocyaneus* as a cause of disease in lettuce and the identity of *B. marginale* with this organism." *Ann. appl. Biol.* xi (1924), 318–23.

(46) Moore, M. H. "Investigations on *Coniothecium*. A progress Report." *Rep. E. Malling Res. Sta. for* 1928, 1929 *and* 1930, II Supp. (1931), 150–6.
(47) Nannfeldt, J. A. "Studien über die Morphologie und Systematik der nicht-lichenisierten inoperculaten Discomyceten." *Nova Acta Soc. Sci. upsal.* Ser. 4, VIII (1932), 94.
(48) Ogilvie, L. and Mulligan, B. O. "Progress report on vegetable diseases." *Rep. Long Ashton Res. Sta.* (1930), p. 135; (1931), pp. 129–30; (1932), pp. 110–15.
(49) Paine, S. G. "'Internal Rust Spot' disease of the potato tuber." (Preliminary communication.) *Ann. appl. Biol.* V (1918), 77–9. See also *Report Intern. Conf. Phytopath. and Econ. Entom. Holland* (1923), pp. 74–8.
(50) Passerini, G. *Erbario Crittigamico Italiano* (1867), Ser. II, No. 148.
(51) Pethybridge, G. H., Moore, W. C. and Smith, A. "Fungus and other diseases of crops 1928–32." *Bull. Minist. Agric., Lond.*, No. 79 (1934), 103–5.
(52) Pethybridge, G. H. "Marsh Spot in pea seeds." *J. Min. Agric.* XLI (1934), 833–49.
(53) Potter, M. C. "On a bacterial disease—White Rot—of the turnip." *Proc. Univ. Durham phil. Soc.* Nov. 1899, 3 pp. See also *Proc. roy. Soc.* LXVII (1901), 442–59.
(54) —— "Bacterial diseases of plants." *J. agric. Sci.* IV (1912), 325.
(55) Quanjer, H. M. "The methods of classification of plant viruses, and an attempt to classify and name potato viroses." *Phytopathology*, XXI (1931), 604.
(56) Ravn, F. K. "Nogle *Helminthosporium*—Arter og de af dem fremkaldte Sygdomme hos byg og havre." *Bot. Tidsskr.* XXIII (1900), 101–322.
(57) Riker, A. J. and Riker, R. S. "Studies on bacteria associated with the Chocolate-Spot disease of broad beans." *Ann. appl. Biol.* XIX (1932), 55–64.
(58) Rostrup, F. G. E. "Nogle Undersøgelser angaaende *Ustilago Carbo*." *Overs. danske Vidensk. Selsk. Forh.* (1890), pp. 1–17. Pub. March 31st.
(59) Schröter, J. C. "Pilze." In Cohn's *Kryptogamen-Flora von Schlesien* (1893), Bd. III, Zweite Hälfte, p. 67. Breslau.
(60) Shear, C. L. "The life history of *Sphaceloma ampelina* de Bary." *Phytopathology*, XIX (1929), 673–9.
(61) Shipley, A. E. "Onion disease at Bermuda." *Kew Bull.* (1887), No. 10, pp. 1–23.
(62) Smith, W. G. *Diseases of field and garden crops* (1884), pp. 45–50. London. See also *Gdnrs' Chron.* XXI (1884), 418.
(63) Stevens, N. E. "Two apple black rot fungi in the United States." *Mycologia*, XXV (1933), 536–48.
(64) Sydow, H. "*Cronartium ribicola:* zur Autorfrage des Pilzes." *Ann. mycol.* XXXII (1934), 115–17.
(65) Thom, C. *The Penicillia* (1930), p. 381. London: Baillière, Tindall and Cox.
(66) Unger, F. "Beitrag zur Kenntnis der bei der Kartoffelkrankheit vorkommenden Pilze und der Ursache ihres Entstehens." *Bot. Z.* V (1847), 315.
(67) Waterman, A. M. "Diseases of rose caused by species of *Coniothyrium* in the United States." *J. agric. Res.* XL (1930), 805–27.
(68) Wollenweber, H. W. "*Fusarium*-Monographie. Fungi parasitici et saprophytici." *Z. Parasitenkunde*, III (1931), 269–516. See also Sorauer's *Handb. d. Pflanzenkr.* Bd. III, Part 2, 5th ed. (1932), 732–819.
(69) Wormald, H. "Bacterial diseases of stone fruit trees in Britain. III. The symptoms of bacterial canker in plum trees." *J. Pomol.* IX (1931), 239–56. See also *Trans. Brit. mycol. Soc.* XVII (1932), 157–69.

ON *CERCOSPORA BLOXAMI* BERK. & BR.

By E. W. MASON

Two fungi are passing in current literature as "*Cercospora Bloxami* Berk. & Br." The first is especially associated with white spot of turnip leaves in this country, but, beyond this fact, has no apparent connection with Berkeley or Broome or Bloxam. It is represented in the Kew Herbarium by the following specimens: G. H. Pethybridge, Devon, 30. x. 24; N. C. Preston, Newport, Salop, x. 24; W. Buddin, Dorset, 12. iii. 26; E. M. Wakefield, Kingthorpe nr. Pickering, Yorks, 18. ix. 30. This is clearly the fungus that was officially recognised by the Plant Pathology Sub-Committee of this Society in 1929 as *Cercospora Bloxami* Berk. & Br. Consideration of Roumeguère's Fungi sel. exsic. 5679, preserved in the same herbarium, shows that it is also *Cylindrosporium Brassicae* Fautr. & Roum., which was described in 1891 on "*Brassica Napo-brassica* Vilm." and which von Hoehnel in 1924 referred to the genus *Cercosporella* as *Cercosporella Brassicae* (Fautr. & Roum.) von Hoehn.

The second is especially associated with cabbage leaves (*Brassica oleracea* and *B. sinensis*) in the tropics,* and, if I am correctly informed, has not been collected in this country. It is represented in the Kew Herbarium by C. G. Hansford, No. 1296, on cauliflower, Kampala, Uganda, June, 1930, and in the herbarium of the Imperial Mycological Institute by W. F. Steven, San Juan, Trinidad, 11. iv. 34. This is *Cercospora brassicicola* P. Henn., as represented at Kew by Baker's *Fungi Malayana*, No. 17 (det. Sydow.).

There is not the slightest difficulty in distinguishing these two fungi: *Cercosporella Brassicae* is white to the naked eye, and, under the microscope, the conidia are typically cylindrical and rounded at both ends. *Cercospora brassicicola* appears to the eye as little blackish tufts; and each conidium, which typically tapers from the base to the apex, has a broad scar right across its base; associated with this, and quite as characteristic, is the presence of brown conidiophores with corresponding broad scars. The only point at issue is to which of these two fungi the name *Cercospora Bloxami* should be applied.

The species was described in *Ann. Mag. nat. Hist.* Ser. 5, IX (1882), 183, as follows:

"1979. *Cercospora Bloxami*, B. & Br. Maculis orbicularibus pallidis; sporis elongato-fusiformibus utrinque acuminatis multiseptatis.—On decaying leaves of turnips, Twycross, Rev. A. Bloxam. Formerly distributed as *Septoria Bloxami*."

* It is also well known in the United States.

There is a specimen at Kew from Berkeley's herbarium, labelled by Berkeley "*Septoria Bloxami* B. & Br." On the envelope is written "on decaying leaves of turnips, Twycross. Unknown to me, A.B." [A. Bloxam]. Three spores have also been figured by the same hand at a low magnification; they appear elongate fusiform, multiseptate (up to 14 cross-septa) and acuminate at the ends. Examination of the specimen shows that the spores figured (and to which the diagnosis undoubtedly refers) are those of the fungus *Alternaria Brassicae* (Berk.) Bolle*; these are there in abundance, but nothing else is to be found.

This then is clearly the type specimen of "*Cercospora Bloxami*", which was overlooked for so long because Berkeley had not relabelled his "*Septoria Bloxami*"; and this specific epithet is accordingly not available for either of the two fungi to which it is being currently applied.

The correct name for the first appears to be *Cercosporella Brassicae* (Fautr. & Roum.) v. Hoehn. in *Ann. mycol.* xx (1924), 193, synon. *Cylindrosporium Brassicae* Fautr. & Roum. in *Rev. mycol.* xxii (1891), 81. From a consideration of their diagnoses, Hoehnel also suggested that *Cercospora* (*Cercosporella*) *albomaculans* Ell. & Ev. (1894) and *Ramularia Rapae* Pim (1897) were synonyms, and (quite rightly) that *Cercospora Bloxami* Berk. & Br. had multiseptate spores, and was therefore distinct. Authentic material of neither *Cercosporella albomaculans* nor of *Ramularia Rapae* is preserved at Kew, but von Hoehnel's surmise is very probably correct.

The correct name for the second species appears to be *Cercospora brassicicola* P. Henn., although in this case it does not seem certain that authentic material has been examined in recent times. The type collection is not preserved in Berlin, but, Prof. Dr E. Ulbrich thinks, may possibly exist in Tokyo, Japan.

* As cited in "The List of Common Names".

THE SPORULATION OF *HELMINTHOSPORIUM AVENAE* AND *ALTERNARIA SOLANI* IN ARTIFICIAL CULTURE

By W. A. R. DILLON WESTON, M.A., Ph.D.
(*School of Agriculture, Cambridge*)

Sometimes there exists a diversity of opinion as to the ease with which a fungus produces spores in artificial culture. Such is the case with the various species of *Helminthosporium*. In view of conflicting statements, Turner and Millard (1) made a detailed study of a culture of *H. Avenae*. A wide range of media was used to embrace varying carbohydrate and nutrient contents, hydrogen-ion concentration and sterilisation methods. No sporulation occurred on any of the cultures excepting on sterilised oat leaves, and then only sparsely. Shortly after this work was published, Dillon Weston (2) stated that abundant sporulation could be promoted by the irradiation of artificial cultures with a Hanovia quartz mercury-vapour home-model alpine sun-lamp, alternating current equipment 200 volts.

It is the purpose of this note to indicate the salient points of this work, and to show how sporulation of the fungus causing Early Blight, *Alternaria Solani*, may be induced by similar methods.

Helminthosporium Avenae

After it had been found that this fungus would sporulate when irradiated with an artificial source of light such as a quartz mercury-vapour lamp, it was necessary to determine the time of irradiation that was necessary at a given distance from the source of light and whether this phenomenon depended upon invisible ultra-violet light or visible white light.

Non-sporing cultures were made in Petri dishes and also in watch-glasses, with watch-glass tops as covers, and were irradiated for ten minutes at a distance of one foot from the source of light. Some cultures were irradiated through the normal Petri plate covers and others through substituted covers made of a proprietary glass named Sanulux that gave a very considerable transmission at 300 $\mu\mu$. Sporulation was abundant in these cultures, while non-irradiated cultures made at the same time and under the same conditions failed to spore. This was confirmed by Mr C. C. Brett, of the Official Seed Testing Station, Huntingdon Road, Cambridge. He irradiated non-sporing cultures for five minutes through Sanulux glass with the result that abundant spore formation took place.

The time period was then reduced and cultures were irradiated for periods between one minute and ten, through the ordinary glass cover and through Sanulux glass. At all periods within this range and under both types of glass, sporulation took place. It was noted that the longer periods of irradiation produced an increase of pigment.

Cultures were also exposed for varying periods to natural irradiation out-of-doors. Some cultures were covered by Sanulux discs, others by the ordinary glass. In all the experiments sporulation took place, but control cultures with blackened surfaces did not sporulate. No attempt was made to determine the time period necessary out-of-doors, since the natural light conditions are variable. On a day during the first week in March, 1933, cultures were exposed for 2 hours 35 min., from 1.55 to 4.30 p.m. Sporulation resulted.

These experiments show that sporulation can be induced by irradiation with natural or artificial light-sources. They suggest, however, that irradiation between 320 and 295 $\mu\mu$ is not the dominant factor in causing spore formation, since it takes place through ordinary glass.

Experiments were then made to see if spore formation could be brought about if the visible light and the shorter ultra-violet rays were screened off. The lamp was screened with a Hanovia diagnosis filter. This cuts out the visible light and transmits ultra-violet between 400 and 300 $\mu\mu$, the main portion of the ultra-violet being furnished by the line 366 $\mu\mu$. Cultures were irradiated for varying periods up to twenty minutes, but no spore formation took place.

As it seemed that sporulation was brought about by visible light and not ultra-violet light, cultures were irradiated to determine the shortest period that would be necessary for exposure.

Cultures made in watch-glasses were exposed for varying periods of from one to sixty seconds. In one series they were irradiated through watch-glass covers and in another series with these covers removed. When exposed directly to the artificial light source sporulation was noted at the exposure made for two seconds and at the periods above this. When irradiated through glass covers, spore formation was delayed and was not noted until the exposure had been made for twenty seconds. Cultures were also made in watch-glasses and placed inside a photographic camera, the lens of which had been removed. This was then placed one foot below the artificial light source. Exposures were made by operating the automatic shutter. Different cultures were exposed for 1/25th, 1/50th and 1/100th of a second and also for periods of from one to thirty seconds. No sporulation resulted. As irradiation through a glass cover had increased the time period necessary, and since spores did not develop after cultures were irradiated for thirty seconds through the diaphragm of a camera,

it was inferred that sporulation depended upon the intensity of the light.

Eight Petri plate cultures were then exposed for fifteen minutes at varying distances from the source of light, the beam being parallel to the cultures. Spore formation took place when the plates were at distances of two, three and four feet—but not further than this. At two feet more spores were formed than at three, and at four feet only a few spores were noted. Controls not irradiated did not spore.

During the course of the experiments the following facts were observed. Spore formation took place about eighteen hours after irradiation. The longer the period that cultures were exposed to light the greater was the degree of pigmentation. If the cultures were not over-exposed the spores germinated normally. If irradiated for long periods the germination was injured.

Alternaria Solani

Potato haulm was received from Dr R. Salaman of the Potato Virus Station, Cambridge, in the summer of 1933. This showed the typical "target-like" lesions of the Early Blight fungus, *Alternaria Solani*. It was, however, difficult at that date to determine the causal organism because spore formation on the material was sparse. After the material had been kept in a moist chamber for ten days spores were noted, and of these some were seen to belong to species of *Alternaria*. Cultures were made but few spores developed. Stevens (3) says: "The mycelium grows luxuriantly within the leaf but spores do not usually form until after the death of the supporting tissues when the conidiophores emerge through the stomata or by rupturing the epidermis. Often no spores are formed and rarely are many present."

As it was thought that light might be a factor influencing spore formation, cultures were irradiated. In order to cut out injurious ultra-violet rays a piece of plate glass $\frac{1}{4}$ in. thick was placed between the source of light to which the cultures were exposed for ten minutes. Eighteen hours later there was profuse sporulation. Cultures exposed out-of-doors also sporulated.

Discussion of results

It appears that visible white light of a high intensity acts as a stimulus for the formation of spores in *Helminthosporium Avenae* and *Alternaria Solani*. If this is so there is some call for the use of an incubator under thermostatic and light control. In the laboratory there must be diminished light intensity, and it may be that this intensity is often not sufficient for the production of spores. An incubator of such a type if built for indoor laboratory use would, of course, require artificial illumination. Alternatively an apparatus could be designed for use out-of-doors in natural light.

Summary

1. *Helminthosporium Avenae* and *Alternaria Solani* sporulate abundantly when exposed to a high light intensity.
2. Sporulation is induced by high intensity of visible white light.
3. Continued high light intensities increase the pigmentation.
4. It is suggested that there may be a need for an incubator under thermostatic and light control.

REFERENCES

(1) Turner, O. M. and Millard, W. A. *Ann. appl. Biol.* xviii (1931), No. 4, 543–6.
(2) Dillon Weston, W. A. R. *Nature*, cxxxi (1933), 435.
(3) Stevens, F. L. *Plant Disease Fungi* (1925), p. 412.

THE GENUS *MILESIA* IN GREAT BRITAIN AND IRELAND

By LILLIAN M. HUNTER

Although the type of the genus *Milesia* was described from Scotland, yet up to the present there are very few records of the species of *Milesia* for Great Britain and Ireland (Grove, W. B., *The British Rust Fungi* (1913), Cambridge; Grove, W. B., "The British species of *Milesina*", *J. Bot.* LIX (1921), 109–10; Grove, W. B., "Mycological notes. VI", *J. Bot.* LIX (1921), 311–15; Wakefield, E. M., "The Belfast Foray", *Trans. Brit. mycol. Soc.* XVII (1932), 5–15; Faull, J. H., "Taxonomy and geographical distribution of the genus *Milesia*", *Contr. Arnold Arb.* II (1932), 1–138). Likewise the only published accounts of life histories of species of *Milesia* from Europe are those of Klebahn (Klebahn, H., "Kulturversuche mit Rostpilzen", *Z. PflKrankh.* XXVI (1916), 257–77) for *M. Blechni* (Syd.) Arth. and Mayor (Mayor, "Eug. Notes Mycologiques VIII", *Bull. Soc. neuchatel. Sci. nat.* LVIII (1933), 23–26) for *M. Kriegeriana* (Magnus) Arth. from *Dryopteris Filix-mas* (L.) Schott. It was my privilege during 1933–4 to make certain studies on rusts in England, and one important part of this work was to investigate the life histories of various species of *Milesia*. A preliminary statement of the results of these investigations on *Milesia* is included here. Accessory to this work much material was assembled both by personal collecting and through the help of others. These collections add to the species already reported for Great Britain and Ireland and to the stages known there for some of the others.

I

Inoculation experiments with basidiospores from the teleutospores of *Milesia* species on their fern hosts were made on various *Abies* species (Hunter, L. M., "Preliminary note on Life History Studies of European species of *Milesia*", *J. Arnold Arb.* XVI (1935)) and spermogonia and accidia of the following rusts were obtained for the first time:

(1) *Milesia Scolopendrii* (Fuckel) Arth. (from *Scolopendrium vulgare* Smith) on *Abies alba* Mill., and *A. concolor* Lindl. & Gord.

(2) *Milesia Polypodii* B. White (from *Polypodium vulgare* L.) on *Abies alba* and *A. concolor.*

(3) *Milesia vogesiaca* (Syd.) Faull (from *Polystichum angulare* Presl.) on *Abies alba.*

(4) *Milesia Kriegeriana* (Magn.) Arth. [from *Dryopteris spinulosa* (O. F. Müller) Kuntze] on *Abies alba, A. concolor* and *A. grandis* Lindl.

Spermogonia and aecidia were also obtained for *Milesia Kriegeriana* (from *Dryopteris Filix-mas*) on *Abies alba*, and on two new hosts, *A. concolor* and *A. grandis*.

In all of the above-named *Milesia* spp. spermogonia appear from twenty-one to thirty days from the time of inoculation, with an average of twenty-three days. The time from inoculation until the appearance of the aecidia varies considerably for the different species as indicated below:

(1) For *M. Scolopendrii*: 67–89 days, with an average of 77 days.

(2) For *M. Polypodii*: 82–89 days, with an average of 86 days.

(3) For *M. vogesiaca*: 99 days.

(4*a*) For *M. Kriegeriana* (from *Dryopteris spinulosa*): 46–59 days, with an average of 53 days.

(4*b*) For *M. Kriegeriana* (from *Dryopteris Filix-mas*): 60–72 days, with an average of 64 days.

Aecidiospores obtained from culture experiments were used in inoculating various ferns with the result that uredospores were obtained for the following species:

(1) *Milesia Scolopendrii* on *Scolopendrium vulgare*.

(2) *Milesia Polypodii* on *Polypodium vulgare*.

(3*a*) *Milesia Kriegeriana* (from *Dryopteris spinulosa*) on *Dryopteris Filix-mas*, *D. spinulosa* and *D. spinulosa* var. *intermedia* (Muhl.) Underw.

(3*b*) *Milesia Kriegeriana* (from *Dryopteris Filix-mas*) on *Dryopteris Filix-mas* and *D. spinulosa* var. *dilatata* (Hoffm.) Underw.

II

Hitherto unreported collections of *Milesia* spp. found in Great Britain and Ireland are listed below:

Milesia Blechni (Syd.) Arth. on *Blechnum Spicant* (L.) With.: Kilmun, Argyllshire, Sept. 26, 1932; Benmore Estate, Argyllshire, Sept. 28, 1932 and Innellan, Argyllshire, Sept. 29, 1932, G. D. Darker (II); Holne Chase, Ashburton, Devon, Apr. 19, 1934, L. M. Hunter (II, III); Glendhu, Glencullen, Dublin, Mar. 29, 1934, H. B. S. Montgomery (II, III); Killakee, Dublin, May 19, 1934, P. O'Connor (II, III); Woodfalls Cross, Downton, Hampshire, Nov. 14, 1933, L. Allen and L. M. Hunter (II); Blackdown, Haslemere, Surrey, Dec. 11, 1933, R. Blockey and L. M. Hunter (II).

Milesia carpatica (Wrób.) Faull on *Dryopteris Filix-mas* (L.) Schott.: Milber Wood, Newton Abbot, Devon, Jan. 1, 1934, L. M. Hunter (II); Milber Wood, Newton Abbot, Devon, Apr. 6, 1934, L. M. Hunter (II, III).

Milesia Kriegeriana (Magn.) Arth. on *Dryopteris Filix-mas*. (L.) Schott.: Benmore Estate, Argyllshire, Sept. 28, 1932, G. D. Darker (II); Milber Wood, Newton Abbot, Devon, Jan. 1, 1934, L. M. Hunter (II); Torquay, Devon, Mar. 25, 1934, E. Milton (II, III);

Watcombe Glen, Torquay, Devon, Apr. 8, 1934, L. M. Hunter (II, III); Powerscourt, Wicklow, May 20, 1934, P. O'Connor (II, III).

Milesia Kriegeriana (Magn.) Arth. on *Dryopteris spinulosa* (O. F. Müller) Kuntze: Benmore Estate, Argyllshire, Sept. 28, 1932, G. D. Darker (II); Duloe, Liskeard, Cornwall, Mar. 31, 1934, M. P. Hall (II, III); Watcombe Glen, Torquay, Devon, Apr. 8, 1934, L. M. Hunter (II, III); Powerscourt, Wicklow, May 6 and 20, 1934, P. O'Connor (II, III).

Milesia Kriegeriana (Magn.) Arth. on *Dryopteris spinulosa* var. *dilatata* (Hoffm.) Underw.: Milber Wood, Newton Abbot, Devon, Jan. 1, 1934, L. M. Hunter (II); Milber Wood, Newton Abbot, Devon, Apr. 6, 1934, and Holne Chase, Ashburton, Devon, Apr. 19, 1934, L. M. Hunter (II, III); Killakee, Dublin, May 19, 1934, P. O'Connor (II, III); Woodfalls Cross, Downton, Hampshire, Nov. 15, 1934, L. M. Hunter (II).

Milesia murariae (Magnus) Faull on *Asplenium Ruta-muraria* L.: Clonsilla, Dublin, Apr. 24 and May 1, 1934, P. O'Connor (II); Powerscourt, Wicklow, May 6, 1934, P. O'Connor (II).

Milesia Polypodii B. White on *Polypodium vulgare* L.: Innellan and Sandbank, Argyllshire, Sept. 29, 1932, G. D. Darker (II); Marldon, Torquay, Devon, Dec. 31, 1933, L. M. Hunter (II); Berry Pomeroy, Torquay, Devon, Apr. 2, 1934 and Marldon, Torquay, Devon, Apr. 23, 1934, L. M. Hunter (II, III); Annahilt, Hillsboro, Down, Aug. 25, 1934, L. M. Hunter (II); Glencullen, Dublin, Apr. 1, 1934, H. B. S. Montgomery (II); Powerscourt, Wicklow, May 6, 1934, P. O'Connor (II, III); Woodfalls Cross, Downton, Hampshire, Nov. 15, 1933, L. Allen and L. M. Hunter (II); Blackdown, Haslemere, Surrey, Dec. 11, 1933, L. M. Hunter (II).

Milesia Scolopendrii (Fuckel) Arth. on *Scolopendrium vulgare* Smith: Duloe, Liskeard, Cornwall, Mar. 31, 1934, M. P. Hall (II, III); Cockington, Torquay, Devon, Dec. 28, 1933, L. M. Hunter (II); Torquay, Devon, Mar. 25, 1934, E. Milton (II, III); Bishop's Walk, Torquay, Devon, Apr. 1, 1934, and Watcombe Glen, Torquay, Devon, Apr. 22, 1934, L. M. Hunter (II, III); Glencullen, Dublin, Apr. 1, 1934, H. B. S. Montgomery (II); Hale, Downton, Hampshire, Nov. 14, 1933, L. Allen and L. M. Hunter (II); Powerscourt, Wicklow, May 20, 1934, P. O'Connor (II, III).

Milesia vogesiaca (Syd.) Faull on *Polystichum angulare* Presl.: Killakee, Dublin, May 19, 1934, P. O'Connor (II, III).

Milesia Whitei Faull on *Polystichum angulare* Presl.: Watcombe Glen, Torquay, Devon, Apr. 8, 1934, and Lincombe Hill, Torquay, Devon, Apr. 23, 1934, L. M. Hunter (II, III); Powerscourt, Wicklow, May 20, 1934, P. O'Connor (II, III).

The uredospore and the teleutospore stages as indicated, of the

following species of *Milesia*, are reported for the first time from England and Ireland:

England: *M. Blechni* (III); *M. carpatica* (II, III); *M. Kriegeriana* on *Dryopteris Filix-mas* (III); *Milesia Polypodii* (III); *M. Whitei* (III).

Ireland: *M. Blechni* (III); *M. Kriegeriana* on *Dryopteris Filix-mas* (II, III); *M. Kriegeriana* on *Dryopteris spinulosa* (II, III), *Milesia murariae* (II); *M. Polypodii* (III); *M. Scolopendrii* (III); *M. Whitei* (II, III).

SOME NEW BRITISH RECORDS OF FUNGI ON WHEAT

CERCOSPORELLA HERPOTRICHOIDES FRON., *GIBELLINA CEREALIS* PASS., AND *OPHIOBOLUS HERPOTRICHUS* (FR.) SACC.

By MARY D. GLYNNE

(*Department of Plant Pathology, Rothamsted Experimental Station, Harpenden, Herts.*)

1. *Cercosporella herpotrichoides* Fron., considered one of the most important of the fungi causing foot rot of wheat in certain parts of France (3, 4) and of the United States (10), and recently recorded in Germany (8), Holland (6), and Denmark (5), has this year been found at Rothamsted.

Pale lesions with dark borders were noticed occasionally on leaf blades and more often on the outer sheaths and leaf bases of wheat on Broadbalk field and an adjacent plot in February. By the latter half of March many plants still had only the outer leaves and sheaths affected, but the fungus was also found on dead leaves, dead tillers and even dead plants and appeared to be responsible for the damage. Dark-bordered lesions were observed at the bases of sheaths and culms in April and May, and were obvious at harvest in August. The disease was fairly common and was found on every plot on Broadbalk field where wheat has been grown every year since 1843. It was found occasionally but not commonly on some of the other fields in which wheat is grown in rotation with other crops. This accords with the general view that the disease increases when inadequate rotation is practised.

Material consisting of dark-bordered leaf and sheath lesions, of dying tillers and dying plants collected several times in the latter half of March all produced abundant spores in damp chambers in a few days. Hardly any spores were obtained from similar material collected at intervals subsequently. This suggests that the duration of sporing may be very short or only possible under particularly limited external conditions.

The spores are hyaline, slightly curved, wider at one end than the other, and attached singly or less often in pairs by their larger ends. They are two- to several-septate, generally five to seven. Measurements of twenty spores showed a variation of $31–80 \times 2{\cdot}2–3{\cdot}3\ \mu$ with an average of $59 \times 2{\cdot}3\ \mu$. These fall within the limits given by Sprague and Fellows (10) of $30–80 \times 1{\cdot}5–3{\cdot}5\ \mu$, most spores being 40–60 μ long.

Cultures from spore suspensions grew on potato dextrose agar at 25° C. first as hemispherical mounds of grey velvety mycelium with a pale edge, later growing out over the agar rather slowly and becoming darker on the under surface. They agreed in appearance with cultures of *Cercosporella herpotrichoides* Fron., obtained from the Centraalbureau voor Schimmelcultures, Baarn, representing isolations by Foëx in France and Oort in Holland.

2. *Gibellina cerealis* Pass., which causes the "white straw disease" in wheat, was found in May on Hoos field, Rothamsted, in the plot on which wheat has been grown alternately with fallow without manure since 1856. The crop was very thin and poor and had suffered much from attack by wheat bulb fly. The fungus caused rotting of tillers and stunting of shoots. It is characterised by dark-bordered elongated lesions on the lower leaf sheaths and basal parts of the culms with a greyish white mycelial felt penetrating and uniting the leaf sheaths, and developing into a stroma with darker cells below. Numerous pale perithecia with black protruding beaks were embedded in the stroma. Only one or two were ripe at the end of May, but from June onwards ripe perithecia were common on affected plants.

Measurements (ten perithecia) showed a variation of 315–600 × 285–570 μ with an average of 432 × 395 μ for the perithecium and 285–455 × 125–220 μ with an average of 367 × 159 μ for the beak. There were numerous filamentous paraphyses among the asci which measured (twenty asci) 90–125 × 13–18 μ with an average of 105 × 16 μ. The uniseptate spores arranged in two rows in the ascus were hyaline at first, becoming honey coloured to hazel and rarely 2–3 celled. Twenty spore measurements showed a variation of 23–36 × 7–11 μ with an average of 30 × 9 μ. Except in the width of the asci these measurements more than cover the range given for *Gibellina cerealis* Pass. Comparison with No. 3669 Rabenhorst-Winter, Fungi europaei, collected by Passerini (Herbarium, Royal Botanic Gardens, Kew) indicate that it is the same fungus.

Germination of spores was not observed, and Ferraris (2) states that they take a long time to mature. Cultures made from the mycelium, however, grew on potato dextrose agar at first as white mounds which later sometimes turned pale grey. Numerous perithecia developed both in the medium and in the aerial mycelium producing asci with typical honey coloured spores in cultures about five weeks old.

The disease was recorded by Passerini (7) in 1886 in Northern Italy, and has recently been noted by Ferraris (2) as occasionally appearing in May doing slight damage. As crop rotation is unfavourable to the disease and is practised in Italy he considers the disease unlikely to become prevalent. Sprague (9) reports it on winter wheat and oats in Oregon, where it occurs locally on some red

sandstone-shale soils, acid in reaction, in the humid coastal regions. He found only immature perithecia and supposes that the dry summers of Oregon are not favourable for their maturation.

3. *Ophiobolus herpotrichus* (Fr.) Sacc. Ripe perithecia were found in March on wheat stubble that had over-wintered in the soil, but no evidence of parasitism was obtained. The perithecia are black with a conical curved beak; the ascospores needle-shaped, multi-septate, measuring (twenty spores) $123–190 \times 2{\cdot}2\ \mu$ with an average of $155 \times 2{\cdot}2\ \mu$. Cultures on potato dextrose agar are whitish grey or brownish, often with dark and light areas. As they become older the under surface becomes darker and ultimately black. The fungus occurs in several European countries together with other fungi causing foot rot of wheat and is generally regarded as a weak parasite of secondary importance. In America(1) it has been found on *Agropyron repens* (L.) Beauv. but not on cereals. In Great Britain it has also been recorded on wild grasses, but not previously on cereals.

I wish to record my thanks to Miss E. M. Wakefield for help in the identification of these fungi.

REFERENCES

(1) Drechsler, C. "Phytopathological and taxonomic aspects of *Ophiobolus*, *Pyrenophora*, *Helminthosporium* and a new genus, *Cochliobolus*." *Phytopathology*, xxiv (1934), 953–83.
(2) Ferraris, T. "Mal bianco degli stelli di Grano." *Riv. agric.*, xxvi (1930), 407–8.
(3) Foëx (E.) and Rosella (E.). "Recherches sur le piétin." *Ann. Epiphyties* (1930), xvi, 2, 51–82.
(4) —— —— "Quelques observations sur le piétin des céréales." *Rev. Path. Vég.* xx (1933), 4–5, 172–87.
(5) Nielsen, O. "Oversigt over Plantesygdomme, 197 Vintermaanederne og April 1934." *Statens Plantepatol.* Forsøg. 5 (1934).
(6) Oort, A. J. P. "Over Voetziekten bij Granen." *Landb. Tijds*, xlv (1933), No. 554.
(7) Passerini, G. "Un' altra nebbia del Frumento." *Boll. Com. agr.*, Parm., No. 7 (1886).
(8) Schaffnit, E. "*Cercosporella herpotrichoides* (Fron.) als Ursache der Halmbruckkrankheit des Getreides." *Phytopath. Z.* v (1933), 493–503.
(9) Sprague, R. "Preliminary note on another foot rot of wheat and oats in Oregon." *Phytopathology*, xxiv (1934), 946–8.
(10) Sprague, R. and Fellows, H. "*Cercosporella* foot rot of winter cereals." *Tech. Bull. U.S. Dep. Agric.* (1934), No. 428, pp. 1–24.

CYLINDROSPORIUM CONCENTRICUM GREV.

By J. R. THOMSON, B.Sc.
(*Mycology Department, University of Edinburgh*)

(With 8 Text-figures)

Introduction

In 1823 Greville described a fungus producing white spots on cabbage leaves. It was first discovered in a garden at Parson's Green, near Edinburgh, but Greville remarks: "It does not seem to be very rare as I have noticed it in various localities since and probably few gardens will be found without it at some time or other of the year." Unfortunately he gives no more precise information as to the distribution of the fungus at that time.

For the reception of this fungus Greville founded the genus *Cylindrosporium*, with the following characters:

> Very minute plants, parasitic on living leaves, without rupturing the epidermis. Sporidia cylindrical, truncate, jointless, naked, free, forming little heaps.

The species he called *C. concentricum* and described it as follows:

> Very white and excessively minute but sufficiently conspicuous from their number and from being disposed in concentric lines. Form most irregular; frequently oblong, lying in the direction from the centre to the circumference, projecting into angles and little eminences and having often one extremity turned up like the end of a canoe. Sporidia very numerous, cylindrical, truncate at both extremities, pellucid without joints and not furnished with any membrane or covering whatever. Turning in decay to a dirty yellow, which always commences in the centre, while new individuals are forming at the circumference. The peculiarity of its cylindrical sporidia, and its situation on the surface of living leaves, fully entitle it to generic distinction.

In 1849 the genus *Gloeosporium* was founded by Montagne. Into it he put the species previously included in *Myxosporium* and *Asteroma* and several new species.

During this time there seems to have been some doubt about Greville's fungus, and there is no record of anyone except Greville having collected it. In 1850, however, it appeared in abundance in market gardens in Northamptonshire. Berkeley(1) immediately recognised it as Greville's fungus and took the opportunity of examining fresh material. He described the fungus as follows:

> The parasite forms, both upon the upper and under surface of the leaf, roundish often confluent patches, varying greatly in size, consisting of little white specks disposed more or less concentrically, those of the centre frequently becoming yellow, and at length fading away, in consequence of the partial decomposition of the leaf which they have affected, while the outer pustules spread from the circumference to the part yet remaining healthy. Occasionally they extend to

the midrib, which is then rapidly destroyed. On close examination it is found that the fungus, each speck forming a distinct individual, is produced between the true cuticle and the cuticular cells.... The cuticular cells, however, are much confused and deranged by the growth of the parasite, which is developed principally at their expense, those of the succeeding layer being very little if at all affected. The mycelium is closely incorporated with the cuticular cells, and appears simply grumous, without distinct structure;...it does not appear to be filamentous. From the top of this mass, on the level of the tips of the cells on which it grows, arise very short delicate sporophores, each of which is surmounted by an oblong, cylindric, often curved, spore, three to five times as long as broad, and containing at maturity from two to three globose nuclei. It is highly probable that each sporophore produces in succession several spores, which are thus pushed forward and in time fill the space between the true cuticle and the cuticular cells, thrusting the former out until it bursts. Partly owing to the successive development of the spores, which are mixed with a viscid fluid, and partly to the contraction of the leaf itself upon the pulpy mass, in dry weather the spores ooze out, kept in connection with each other by their attendant mucilage, and drying as they are exposed to the air, form rude irregular short tendrils. These tendrils are in their turn softened again by moisture, and after a time fall down, forming a little pellicle on the leaf, the edges of which are often turned up like a little boat or canoe, as observed originally by Dr Greville. The spores, it should be observed, are not truly truncate, as they appeared to Greville when examined by the old imperfect compound microscope, but rounded and obtuse.

Berkeley considered that Greville was correct in founding a new genus, but that *Cylindrosporium* was identical with *Gloeosporium*. He added:

> It is but proper courtesy to adopt his (Montagne's) name unless he should think fit to restore that of Greville as to the identity of which there is now no doubt.

It was therefore proposed that the fungus should be called *Gloeosporium concentricum* Berk. & Br.

Saccardo (6) adopted Berkeley's suggestion, though expressing some doubt about it, and in his *Sylloge Fungorum* Greville's fungus is given as *Gloeosporium concentricum* (Grev.) Berk. & Br. (=*Cylindrosporium concentricum* Grev.). He said that: "From Greville's figure it appears to be a doubtful species."

Considerable confusion has arisen as to the genus *Cylindrosporium* and it is difficult to trace its history. The first to use Greville's name was Unger, who added parasites on the celandine and on *Brassica* spp. under the impression that they were of the same genus as Greville's fungus. These fungi had filiform spores and it is difficult to understand how this confusion arose, for, though Unger probably never saw Greville's actual specimen, he must have seen his description. When Berkeley removed *C. concentricum* Grev. to the genus *Gloeosporium* he realised that Unger's genus was quite distinct from Greville's.

Saccardo (6) gave a clear definition of *Cylindrosporium* Ung. which might have been expected to prevent any confusion. He defined it as a *Gloeosporium* with filiform conidia and certainly a conidial stage

of *Entyloma*. Unfortunately, according to Diedicke(3) and von Hoehnel(5), some of the species included by Saccardo were not conidial stages of *Entyloma*, and other species, not *Entyloma* forms, have been added since.

In 1924 von Hoehnel(5) investigated the thirty-three species then attributed to *Cylindrosporium* Ung. em. Sacc. (non Grev.). He found that they could be divided into two groups—Melanconieae species and Sphaeroidiae species, the former including conidial forms of *Entyloma* and *Doassansia*. The species were all removed to other genera, five of which were new.

Having demolished the genus *Cylindrosporium* Ung., von Hoehnel proposed to re-establish the genus *Cylindrosporium* Grev. with *C. concentricum* as its only species. While this attitude may be tenable, the reasons which von Hoehnel gives for adopting it seem rather flimsy, especially as he had never seen a specimen of the fungus.

Von Hoehnel says: "Dieselben (Berk. & Br.) fanden, dass der Pilz, entgegen der Angabe Grevilles, sich unter der Kutikula wie ein *Gloeosporium* entwickelt und stellten daher den Pilz in diese Gattung. Unter Kutikula ist hier wohl die Epidermis zu verstehen."

This refers to a short note(2) on Greville's type specimen, and it is obvious that he cannot have seen Berkeley's paper(1) published a year later (quoted above). His description of the fungus differs from Greville's in only one point—the spores are described as having rounded ends while Greville described them as truncate. Moreover, Berkeley was particularly emphatic as to the position of the acervulus —"between the true cuticle and the cuticular cells"—so that the question of confusion between cuticle and epidermis does not arise.

Ignoring Berkeley and Broome's description, von Hoehnel's conclusion is based on that of Greville which is accepted as being correct. From the habit of the fungus, its snow white fructifications and the probable formation of the spores in loose chains, he concludes that it could not be a *Gloeosporium*. The catenulate arrangement of the spores is deduced from Greville's statement that the spores are truncate, which was denied by Berkeley. It must be admitted, however, that from Greville's inadequate description alone it would be difficult to state definitely that it was not a *Gloeosporium*.

Further, von Hoehnel says: "Greville nennt den Pilz eine sehr ungewöhnliche Pflanze, was er gewiss nicht gesagt hätte, wenn es sich um ein *Gloeosporidium* gehandelt hätte." But the genera *Gloeosporium* and *Gloeosporidium* were not established till many years after Greville's time and it may be presumed that fungi of that type were not then well known.

Investigation

A fungus forming white spots on cabbage leaves is fairly common in gardens in the Edinburgh district and can frequently be seen on the outer leaves of cabbages exposed for sale in the town. It is generally assumed to be *Gloeosporium concentricum* (Grev.) Berk. & Br. Inquiries have shown that its distribution is fairly general in Scotland and England, though nowhere abundant. Cauliflowers and broccoli are also attacked. The type specimen of Greville's *Cylindrosporium concentricum* is in the herbarium of the Royal Botanic Garden, Edinburgh. It was decided to investigate the fresh material and the type specimen and to find what relation, if any, there was between them.

Fresh material

Fresh material was easily obtained in October. The fungus forms white spots on either surface of the leaf, but more commonly on the under surface. The spots are grouped in concentric circles and each group is from 1 to 2 cm. in diameter (Fig. 1). They appear generally

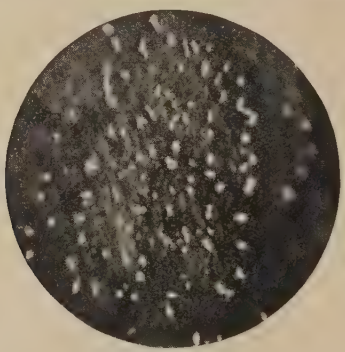


Fig. 1. Group of fructifications on cabbage leaf. ×5.

between the main veins, but may also be found on the veins. As new spots are formed on the outside of the group, the spots in the centre disappear and the leaf turns yellow and then black, and finally only a number of concentric black lines is left. Each group of spots is quite distinct, but the groups may run into each other and overlap. The fungus is found on the outer leaves, which are already beginning to yellow, and seems to have no serious effect on the host. A cabbage which had its outer leaves infected was kept under observation. Some of the adjacent leaves became infected, turned yellow and dropped off, but infection never reached the heart. Finally the fungus dis-

appeared altogether and the cabbage appeared perfectly healthy and very vigorous. The fungus can live saprophytically on dead leaves. As cabbages grow at all times of the year there is no difficulty in the fungus finding a host.

The spots are minute, being less than 1 mm. across. Under the lens, a spot appears as an irregular gelatinous white mass oozing from a slit in the surface of the leaf. This exudation sometimes takes the form of a tendril, but more generally the spots are irregular and may take the form of a canoe, as described by Greville (Fig. 2).

Fig. 2. Fructifications (spots) as seen on leaf surface. ×40.

While the white spots appear to ooze out of a slit in the leaf surface, there is no apparent rupture or tearing of the epidermis.

Each spot consists of a mass of spores. The spores are cylindrical, sometimes curved, with rounded ends and generally two oil drops. They are 8·5–15 × 2·5–5·5 μ, with an average size of 11 × 4 μ. In January spores were found with an irregular number of transverse bands. This was due to enlargement of the oil drops and the formation of the protoplasm into bands between them (Fig. 3).

Sections were cut of infected leaves. In section the fructification appeared as an irregular grumous mass surmounted by a heap of

spores (Fig. 4). The position of the spores in irregular chains suggested that they were budded off in succession from the basal hyphae, though no section could be obtained showing the process of budding. Where the lamina was infected the tissues were somewhat disorganised, but

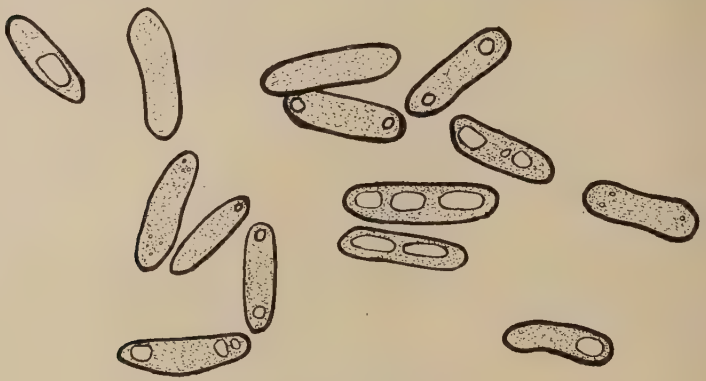


Fig. 3. Spores. × 3600.

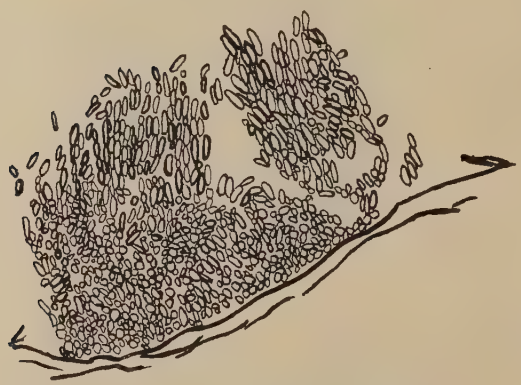


Fig. 4. Section of fructification from leaf lamina. × 360.

the fungus was obviously superficial. Sections through fructifications over a vein, however, showed that they were subcuticular, and no trace of penetration through the epidermal walls could be found (Fig. 5). Sections were obtained showing hyphae within the cuticle between fructifications. The hyphae appeared singly or in pairs, but

occasionally several were clumped together and may have represented a young fructification (Fig. 6).

It will be seen that this fungus agrees exactly with Greville's description (as far as it goes) of *Cylindrosporium concentricum*, except for the form of the spores which Greville gave as truncate. This difference, however, was plausibly explained away by Berkeley (see p. 124). It also agrees with Berkeley's description, though no definite

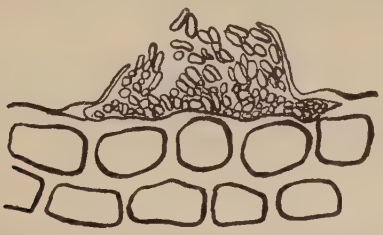


Fig. 5. Section of fructification from vein, showing subcuticular position. × 360.

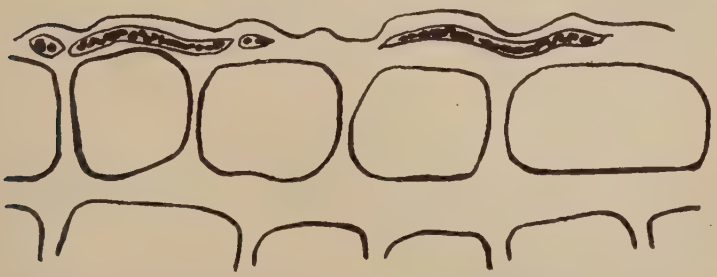


Fig. 6. Section of epidermal cells, showing hyphae within cuticle. × 1270.

sporophores could be found. Berkeley figured the sporophores but does not show them in his figure of the acervulus. This figure shows a flat layer of fungal tissue surmounted by a single layer of spores with no definite attachment. A very similar appearance is seen in hand sections of the fresh material in which the upper spores are knocked off leaving only a single layer.

Saccardo described *Gloeosporium concentricum* as having truncate spores, and this is the only point of difference between his description and the fungus examined.

There can be no doubt that this fungus and Greville's are identical.

Type specimen

The type specimen bears the legend "*Cylindrosporium concentricum* nov. gen. mihi. On *Brassica oleracea*. Balmuto [Fife], May 1822. Miss Boswell". It consists of a small piece of cabbage leaf with pale-coloured areas but showing no external signs of the fungus.

Sections were cut and fructifications were found. They were quite similar to the fructifications on fresh material, but flattened out owing to herbarium treatment (Fig. 7). Owing to the disorganisation of

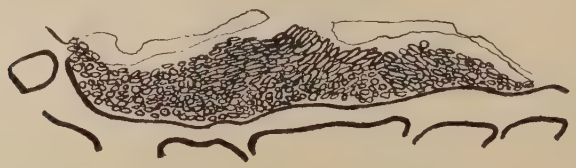


Fig. 7. Section of fructification from Greville's type specimen. ×360.

the tissues it was impossible to determine their exact position, but they appeared to be superficial. Free spores could not be obtained so the spores were measured in the sections and compared with spores in sections of the fresh material after similar treatment:

	Type specimen	Fresh material
Spore size range	5·5–8·0 × 1·6–2·5 μ	5·5–8·0 × 1·6–2·2 μ
Average	6·6 × 2 μ	6·6 × 2 μ

It should be noted that the spores are not truncate but have rounded ends. There is a co-type specimen in the Kew Herbarium and free spores have been obtained from it. These spores show this character very clearly.

This investigation of the type specimen confirms the conclusion that the fungus found on the cabbage and Greville's fungus are identical.

Cultures

Spores from fresh material were germinated in water and dilute cabbage extract. They germinated by a single terminal or sub-terminal germ tube.

Attempts to culture the fungus on malt and oatmeal agar failed. The spores germinated but soon died off. A medium was therefore made up with cabbage extract. 200 gm. of fresh cabbage leaves were boiled in water for 7½ hours, the extract filtered and made up to 200 c.c. The best results were obtained on a medium containing 5 per cent. of this extract.

The fungus grows very slowly, ultimately forming a growth 1–2 cm.

in diameter. The mycelium, which is greyish, grows within the medium, but frequently a white cottony mycelium is produced on the surface. Later, white gelatinous pustules appear, very like the spots on the cabbage leaf. These pustules consist of heaps of spores as on the cabbage.

The spores are budded off irregularly from the hyphae, there being no specialised sporophores. They are produced laterally or terminally in succession and lie loosely in irregular chains (Fig. 8).

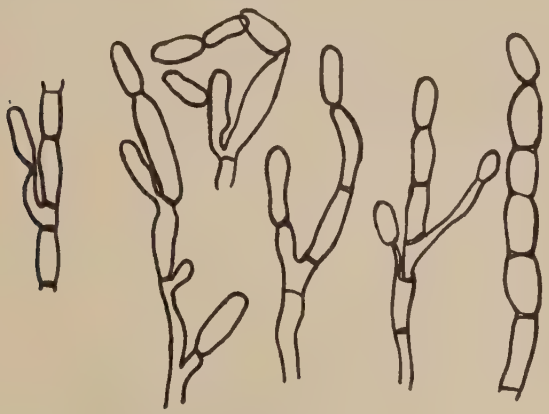


Fig. 8. Spore formation in culture. × 1800.

At a late stage small black sclerotium-like bodies may be produced in culture. They are spherical or lobed and no definite internal structure could be made out. They may possibly be immature pycnidia, but no spores could be found in them. In its final form, black radiating lines appear in the growth giving it a dark appearance, but the periphery remains grey.

Discussion

The question arises as to the systematic position of the fungus. Berkeley and Broome regarded it as a *Gloeosporium* and were followed in this by Saccardo. The alternative is to retain Greville's genus *Cylindrosporium* and to regard it as monotypic as suggested by von Hoehnel. Certainly there is nothing in the description of the genus *Gloeosporium* as given by Saccardo which definitely excludes the fungus from that genus, except the subcuticular position of the acervulus, and Saccardo included it in spite of this. On the other hand, it is certainly not a typical *Gloeosporium*. The heaping up of the spores

in clumps is unusual, and there seems to be no record of another subcuticular species in the genus. *Gloeosporium* species have typically a shallow fructification bearing a shallow layer of spores, while in this fungus the spores appear to be budded off in chains and adhere together in a heap above the fructification. Cultures have shown that this arrangement of the spores is due to their being budded off in succession from the hyphae. von Hoehnel thought that its habit, the whiteness of the fructifications, and the probable arrangement of the spores in chains (deduced from the truncate spores) were sufficient to distinguish this fungus from *Gloeosporium*. While these characters alone seem inadequate, when they are combined with the subcuticular position of the acervulus, the formation of the spores by irregular budding, and the confirmation of the catenulate arrangement of the spores (though they are not truncate), there seems good reason for retaining Greville's genus *Cylindrosporium*.

Summary

Cylindrosporium concentricum Grev. was described by Greville in 1823.

Berkeley removed it to the genus *Gloeosporium* Desm. & Mont., and was followed in this by Saccardo.

von Hoehnel in 1924 removed all the species from *Cylindrosporium* Ung. em. Sacc. (non Grev.) and re-established the genus *Cylindrosporium* Grev. though he had not seen Greville's fungus.

A fungus parasitic on cabbage leaves is described and compared with the type specimen of Greville's fungus. It is shown to be identical with the type specimen and to agree in external characters with Greville's description.

Cultures of the fungus were obtained.

The fungus is not a typical *Gloeosporium*. The description appears to support von Hoehnel's view that the genus *Cylindrosporium* Grev. should be re-established with this fungus as its type species.

I am indebted to Dr Malcolm Wilson for suggesting this investigation and for his supervision.

REFERENCES

(1) Berkeley, M. J. "Additional observations on the white rust of cabbages." *J. R. hort. Soc.* VI (1851), 117–21.

(2) Berkeley, M. J. and Broome, C. E. "Notices of British fungi." *Ann. Nat. Hist.* XL (1850), No. 441.

(3) Diedicke, H. "Nach einige Leptostromaceen, die Nectrioideen, Excipulaceen & Melanconieen. No. 5. Melanconieen." *Ann. mycol.* XI (1913), 536–45.

(4) Greville, R. K. "*Cylindrosporium concentricum.*" *Sc. Crypt. Fl.* I (1823), No. 27.

(5) Hoehnel, F. von. "Beitrag zur Kenntnis der Gattung *Cylindrosporium* Grev." *Ann. mycol.* XXII (1924), 191–203.

(6) Saccardo, P. A. *Syll. Fung.* III (1884), 701.

STUDIES IN THE GENUS *USTULINA* WITH SPECIAL REFERENCE TO PARASITISM

II. A DISEASE OF THE COMMON LIME (*TILIA VULGARIS* HAYNE) CAUSED BY *USTULINA*

By W. H. WILKINS, M.A.

(*Senior Demonstrator and Mycologist in the University Department of Botany, Oxford*)

(With Plate I and 8 Text-figures)

I. Introduction

As stated in a previous communication (26), the main objective of these studies is investigation into the economic aspect of the temperate form of *Ustulina* in relation to standing timber—especially beech. Beech was chosen because the timber is important and because, in my opinion, *Ustulina*—which is characteristically abundant on that tree—causes a timber rot which is sufficiently serious to merit attention.

Under the general heading, however, the above-mentioned disease of lime is a specific case which occurred locally, and, as it affords excellent material for relevant investigation as well as opportunity for testing experimental methods, will be considered first and is the only aspect of the problem dealt with in the present paper.

Lime is characteristically immune to any form of fungus disease and particularly so to disease of the "timber rot" type; it is not therefore surprising to find that there appear to be only six previous records of *Ustulina* on this host. The first three of these, Lind (13) from Denmark, Bizzozero (1) from Italy, and Sydow (22) from Germany, merely indicate growth of the fungus on the tree with no suggestion of parasitism. Of the last three, however, Wehmer (24), in Germany, is doubtful whether or not it causes disease; Van Overeem (23) says that it occurs in France, is emphatic that it causes disease of lime in that country, but gives no circumstantial details; while Patouillard (16), from France, definitely states that *Ustulina* is parasitic. He says*:

> Ce champignon bien connu à l'état saprophyte paraît avoir causé la mort de deux troncs de Tilleul dans l'Ain, en attaquant par la base, au niveau du sol. Sur une hauteur de 20 à 30 cent. ces deux troncs étaient recouvert d'une couche continue du parasite, sauf sur une largeur de 10 cent. qui est restée saine.
>
> Le bois est complètement envahi par le mycelium et a pris une consistance très

* This important reference does not appear in the literature list given in Part I, as it was verified too late to be included in that paper.

molle, jusqu'au centre des arbres, en sorte qu'une simple coup de vent a pu les faire tomber.

L'Ustulina est très fréquent sur les vieilles souches voisines tant sous sa forme ascophore qu'à l'état conidifère mais toujours en saprophyte.

Dans le cas actuel il est nettement parasite.

This scarcity of previous record of disease of lime by this fungus does not entirely eliminate the possibility of its being a pathogen of economic importance as the disease may have been overlooked—a factor which I should like to suggest is also largely responsible for its non-recognition as a pathogen on beech, though this is even less understandable. A second and more probable reason is that the disease symptoms of *Ustulina* may have been credited to another fungus of the "black-line" type.

No standard text-book on the diseases of trees from the time of Hartig(8) in 1882, to the *Forest Pathology* of Hubert(12) published in 1931, makes any reference to *Ustulina* as a wood destroyer.

I have come across three lime trees which appear to have been diseased by *Ustulina*:

(1) A tree brought down by the wind in the Botanic Gardens at Oxford.

(2) The tree next to the above which is obviously infected but is still standing.

(3) A very diseased tree in Blenheim Park, Woodstock. This tree is quite hollow, shows all the signs of *Ustulina* disease, and no fructifications other than those of this fungus were found on the tree.

Of these trees only the first mentioned was available for experimental purposes.

II. Preliminary examination of the tree

The tree was a well-grown specimen about seventy years old, and, apart from a few dead branches, the crown appeared to be perfectly healthy. Closer examination revealed the fact that the trunk was less sound, there was a wound on the north side—caused when the tree was struck by lightning about 1880—extending from ground level to a height of about twelve feet. The exposed wood of the wound was soft and rotten, but the rest of the trunk seemed to be perfectly normal. There were no sporophores or visible fructifications of any fungus except those of the saprophytic *Peniophora quercina* (Pers.) Cke. on some of the dead branches, and those of *Ustulina vulgaris* Tul. which were growing on the surface of the exposed wood of the wound. There was no evidence of the rhizomorphs of *Armillaria mellea*.

When the tree crashed the base was badly smashed up from ground level, where it broke off, to a height of about six feet; it was apparent that, except for a few inches of sound wood on the south side, all

the base of the trunk was completely rotten, obviously diseased by fungi or bacteria. The rotten wood was soft and crumbly and thoroughly permeated by "black lines".

III. Isolation of the causal organism

By means of a borer, many sterile isolations were taken from the diseased timber in various parts of the stem and roots. The isolations were grown on media known to be favourable to the growth of most fungi and many bacteria, but all isolations produced only remarkably pure cultures of *Ustulina vulgaris*. Eventually the identity of the causal organism with this species of fungus was presumed on the following grounds:

(1) Proximity of undoubted fructifications of *Ustulina* to the diseased timber.

(2) Similarity of cultures isolated from the diseased timber with those of standard cultures of *Ustulina*. This diagnosis was confirmed by Mr Cartwright (Head, Mycology Department, Forest Products Research Laboratory, Princes Risborough), both from cultures supplied by the writer as well as from his own independent isolations from the timber.

(3) In spite of repeated trials no other fungus could be isolated.

(4) The details of the disease conditions corresponded very closely with those described, as caused by *Ustulina* on certain tropical trees, by other investigators.

(5) Artificial infection with the isolated fungus into sound lime wood produced only symptoms of disease identical with those occurring in the naturally infected wood. This was true in inoculation into dead wood as well as in artificial infection into living trees.

(6) The fungus was re-isolated from the artificially infected wood—dead and living—and again pure cultures of *Ustulina* were obtained.

(7) Artificial inoculation into lime with a culture from authentic *Ustulina* spores produced exactly the same symptoms as the above.

The invariable presence of *Ustulina* in the diseased wood does not preclude the possibility of its being a secondary rather than a primary infection, but it is suggested that the evidence produced in the course of this paper tends to disprove this hypothesis.

IV. General observations on the type and extent of the disease

(1) *Macroscopic examination*

Through the kindness of the Bursar of Magdalen College, I was able to have the whole tree for the purpose of investigation, and both stem and root were cut up into sections.

In the sections of the stem and root the so-called "sound wood"

was the normal wood of the lime, and, structurally, calls for no special comment. It surrounds the discoloured and diseased wood on all sides except that which is completely decayed out to the bark. Cultures of sterile borings from this wood produced no evidence that it contained fungus hyphae.

(*a*) *The stem.*

The base of the tree was badly smashed up when it broke off, and the first section which could be cut corresponded to a height of about six feet above ground level; other sections were cut as shown in the following table and will, in future, be referred to by these numbers:

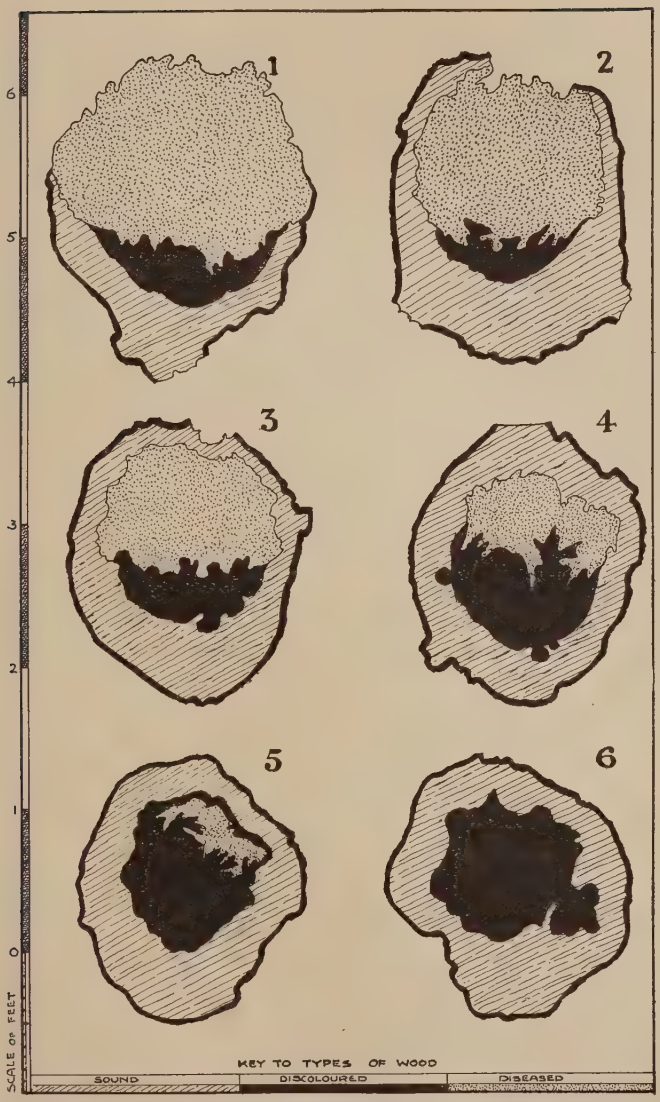
Number of sections ...	...	1	2	3	4	5	6
Height in feet ...	...	6	10	12	14	15	18

Text-fig. 1, diagrams 1–6, shows diagrammatically the appearance of each of the sections cut at the above levels. The diagrams are from actual tracings of the sections reduced to one-eighth natural size. All the sections are arranged so that the side which originally faced north is uppermost. Plate I, fig. 1, shows a photograph of section 1.

In each of the first five sections, areas representing three distinct types of wood are recognisable; these three types will be referred to as: (i) sound wood; (ii) discoloured wood; (iii) diseased wood.

The sixth section—at eighteen feet—showed only the first two types. All the sections show the relative extent and distribution of the different types of wood in the trunk, and the discoloured and diseased wood will be discussed separately in greater detail.

(i) *The discoloured wood of the stem.* This is brownish red and is, therefore, sharply marked off from the diseased wood on the one hand and the sound wood on the other, as both of these are light coloured. The line of demarcation between the discoloured wood and the sound wood is often specially emphasised by a narrow zone of the deeper colour which is found on the outer edge of the former. The successive sectioning of the trunk brought out the fact that the discoloured wood extended to a height of about twenty-four feet, *i.e.* about eight feet beyond the height actually reached by the diseased wood. In transverse section this discoloured wood shows a tendency to occupy a more or less central position in the stem, simulating heart-wood (lime is a sap-wood tree), and seems to be identical in appearance with the type of discoloration popularly known as "dark-heart", "black heart", "red heart", etc., which may exist as a physiological or pathological condition in all kinds of trees. It is more evident on that side of the diseased wood which is farthest from the (presumed) point of infection; this suggests that (*a*) it was present in the stem before the disease started, or (*b*) that it may have been



Text-fig. 1. Transverse sections of the lime stem, cut at different levels (explanation in the text).

produced by the advance mycelium of the fungus and so be a preliminary symptom of decay. In neither longitudinal nor in transverse section does it show any regional relation to the annual rings, but, as its outer edge tends to follow the course of the vessels, in longitudinal section this edge appears as a more or less straight line. In the lowermost sections it has been largely "overrun" by diseased wood and so appears merely as a comparatively narrow zone, and even this may be present at one part of the circumference only (Text-fig. 1, diagrams 1–4). In the uppermost sections it forms a relatively wider zone entirely surrounding the diseased wood (diagram 5), until, in the highest section of all, it alone occupies the central region of the stem. It seems, in fact, that the discoloured wood bears a closer relation to the stem than it does to the fungus, for its outline is more or less concentric with the outline of the stem, whereas it shows no definite relation to the outline of the diseased area.

Discoloured wood of the type mentioned above has been noted by Hubert ((11), p. 533) on a species of lime infected by *Pholiota adiposa*, and has also been referred to by Sharples ((19), p. 12) in connection with *Ustulina* disease of rubber.

Numerous sterile borings from this wood were cultured but gave no evidence that the wood contained mycelium.

(ii) *The diseased wood of the stem.* This extends up the trunk from ground level to a height of about sixteen feet. Reference to Text-fig. 1, diagrams 1–5, will show that towards the base of the tree the diseased wood occupies the greater part of the cross-section, but its area gradually decreases from the base upwards till, at a height of eighteen feet, it is no longer present; at the same time it tends to become more centrally placed in the stem, indicating a probable preference for the older tissues or for the discoloured wood. In the transverse direction, the appearance of the diseased area suggests a progressive spread of the mycelium from the wound on the north side, and it is obvious that the disease spreads more rapidly in a longitudinal than in a transverse direction.

The diseased wood is light in weight, crumbly in texture and of a lighter colour than normal lime wood. On the more completely diseased sections—in general on sections nearer the base than the lowest section illustrated in the diagrams—the wood is typically permeated by "black lines". These are irregularly distributed and presumably make their appearance as the wood "dries out" as the result of exposure, produced naturally or artificially. They are found in wood which is on the exposed surface of the trunk but not in the diseased wood which is situated some distance from the outside. On allowing the sections to dry naturally in the laboratory, however, black lines became apparent where they had not been noticed previously. They often extended across the wood more or less parallel

to and a short distance from the cut surface, and a black line was almost invariably produced (after drying out) at the junction of the diseased and the discoloured areas. The lines sometimes enclosed irregularly distributed areas of wood of a dark brown colour.

Though definitely and invariably associated with decay by *Ustulina*, these black lines are not a specifically diagnostic character, as they are present in many kinds of diseased timber, being produced by some thirty different species of fungi.

The above facts on the appearance of the diseased wood as seen by the naked eye agree in all essential details with those described for *Ustulina zonata* on rubber by Sharples (19) for Malaya, by Steinmann (21) for the Dutch East Indies, and by Weir (25) in the Amazon Valley.

As stated previously, cultures of *Ustulina* were consistently produced from sterile borings of this type of wood, though less readily from the older parts than from the region nearer to the edge of the advancing mycelium.

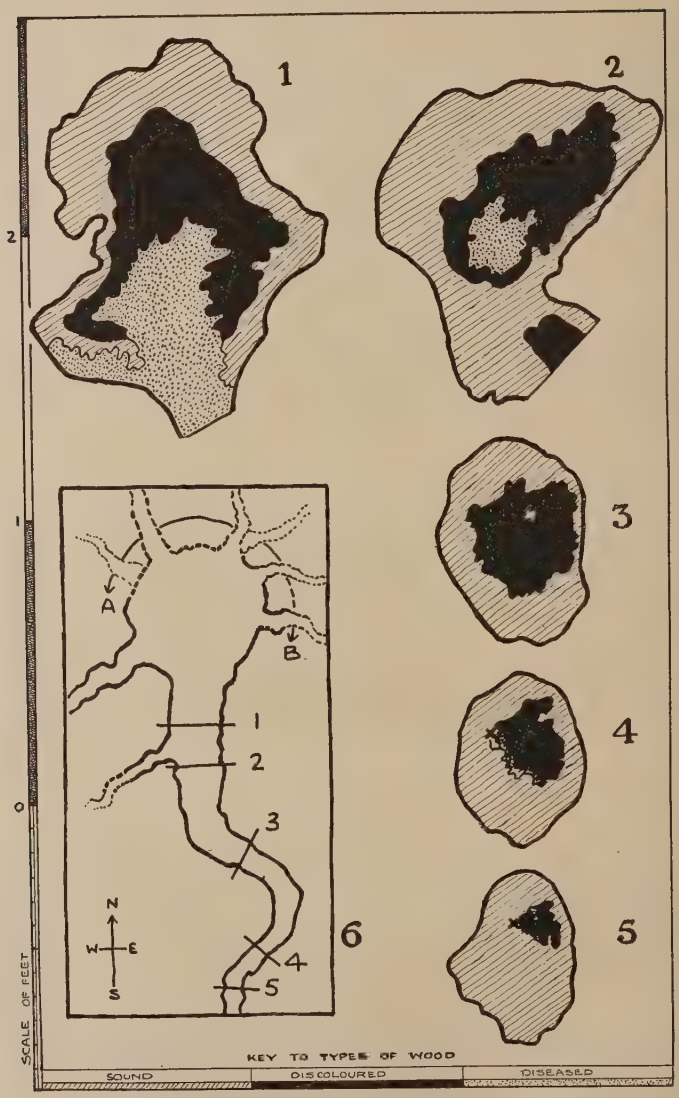
(*b*) *The root.*

The root system of the tree was also examined. Text-fig. 2, diagram 6, shows the general lay-out of the roots as they appeared after excavation. There was no tap root, merely a bunch of fibrous roots about three feet deep, the largest being about 2½ inches across. The roots on the north side of the tree—from *A* to *B* on the diagram—that is to say the roots arising from below the wound on the stem, were quite rotten and broke when dug up. On the whole the roots were small; there was one large lateral root on the south side and growing towards the south, and a smaller lateral on the south-west. All these roots were infected by *Ustulina*. The largest root (south side) was sectioned as follows:

Number of section ...	1	2	3	4	5
Distance from trunk ...	9″	1′ 3″	2′ 6″	4′ 6″	5′ 3″

The root sections showed the same three types of wood as did the stem, and Text-fig. 2, diagrams 1–5, shows the relative extent and distribution of these types as seen in transverse section. As in the stem, the diagrams are from tracings of the timber, but here are reduced to quarter natural size. All the diagrams (except diagram 6) are arranged so that the morphologically upper side of the root is uppermost. Plate I, fig. 2, is a photograph of root section 1. The first two sections show all the types of wood, but on the last three sections, only sound wood and discoloured wood are represented.

(i) *The discoloured wood of the root.* From the diagrams in Text-fig. 2 it will be seen that this is particularly well represented in the root. It is rather darker in colour than the corresponding area in



Text-fig. 2. Transverse sections of the lime root cut at different levels (explanation in the text).

the stem—this is well shown in Plate I, fig. 2—though here the deeper colour is emphasised rather out of proportion due to the greater moisture content of the root at the time of taking the photograph—the discoloration always being more definite when the wood is damp. This discoloured wood extends down the root for a distance of about five feet six inches, *i.e.* about three feet beyond the diseased wood. It exhibits the same tendency to be restricted to the central regions that was noticed in the stem and, especially in the upper part of the root (Text-fig. 2, diagrams 1 and 2), its outline follows that of the periphery of the root sufficiently closely to suggest a physiological connection. The fact that there is no relation between the distribution of the discoloured area and the annual rings is well emphasised in the more distal part of the root—as shown in Text-fig. 2, diagrams 3, 4 and 5—where the centre of the root is marked with an *X*. Though this discoloration sometimes approaches very close to the edge (Text-fig. 2, diagram 3), yet it never extends right out to the bark.

The culturing of sterile isolations from this wood did not produce any mycelium.

(ii) *The diseased wood of the root.* There is, of course, some doubt as to the exact position of the original infection, but it would appear that the fungus travels less quickly in the root than in the stem in both the longitudinal and the transverse direction. There was no evidence of any diseased wood at two feet from the junction with the trunk, and the area of this type of wood in the cross-section of the most diseased part is comparatively small. The diseased area is found on the lowermost side of the root and, as in the stem, it spreads towards the centre. In all structural details the diseased wood of the root is similar to that of the stem. Black lines, which are not evident in the freshly cut timber, make their appearance as the wood dries out.

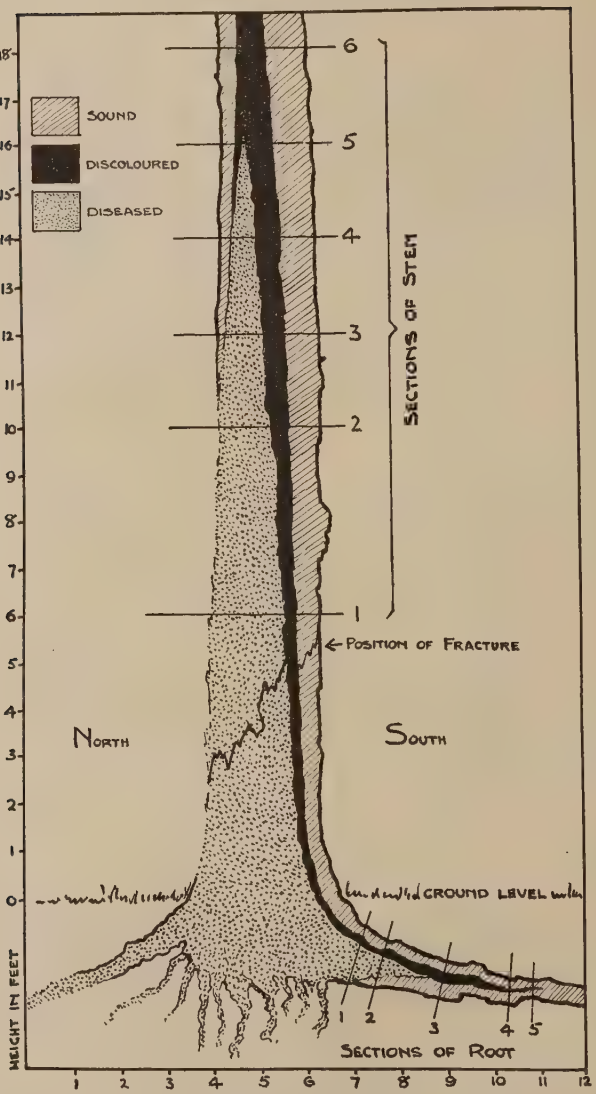
Sterile borings from this wood consistently produced cultures of *Ustulina*.

(*c*) *Distribution of disease in the tree.*

From the successive transverse sections of the stem and root and from the records obtained when these are cut longitudinally, it is possible to reconstruct the general distribution of the diseased tissues in the tree as a whole. Such a reconstruction is illustrated diagrammatically in Text-fig. 3, which is self-explanatory. This is a typical example of the effect of *Ustulina* as a wood-destroying fungus.

(*d*) *Superficial mycelium.*

After the sections had been cut for about a week, a dense mycelial growth appeared on the surface of certain sections of both stem and root. It grew out of the diseased wood and was never found on any



Text-fig. 3. Reconstruction of a longitudinal section through the tree (explanation in the text).

other type of wood; the outline of this mycelium followed the outline of the diseased wood exactly. This superficial growth showed first and grew most luxuriantly on the most distal sections of stem and root, *i.e.* the mycelium seems to be most active on the growing margin. This was confirmed by observation of the transverse sections, for the fungus always appeared first on the extreme edge of the diseased wood where it bordered on the discoloured wood, the part farther from the discoloured wood showing a much more scanty growth. At a later date the mycelium was to be found on the lower sections but—in the stem—it became progressively less vigorous towards the base of the trunk, that is to say on the more completely diseased wood. Plate I, fig. 3, shows a "close up" of this superficial mycelium as it appeared on the uppermost root section. This is a typical example of the appearance of *Ustulina* mycelium as seen in nature, and this is, moreover, almost identical with its cultural aspect.

This type of superficial mycelium is figured by Schrenk ((18), Plate V) in connection with a disease of ash caused by *Polyporus fraxinophilus*, and also by Heald ((9), Fig. 246, p. 784), who shows a surface growth of the mycelium of *Stereum purpureum* on cross-section of apple timber.

(2) *Microscopic examination*

Before going on to the more detailed examination it may be well to state certain assumptions which will tend to explain the course of the investigation. In a section of the diseased trunk, *e.g.* section 2 in Text-fig. 1, it is assumed that:

(*a*) Infection took place at a point in the region of the wound on the north (uppermost) side.

(*b*) The spread of the mycelium from this point was fan-wise in the general direction of the opposite side of the stem, that is through the discoloured wood if that was already present, or converting the sound wood into discoloured wood as it penetrated it. In the latter, one is assuming discoloration to be the initial stage of decay.

(*c*) The actual decay, which proceeded more slowly, in the same sense, then gradually converted the discoloured wood into diseased wood, *i.e.* disintegration is the ultimate stage of decay.

With the idea of examining the timber from this point of view a strip about four inches wide was cut down the centre of stem-section 2. Plate I, fig. 4, shows a photograph of this strip in transverse and in radial section. The strip is arranged so that the sound wood is uppermost (the examination being carried out from the periphery inwards), and all the subsequent drawings have the same orientation.

From this strip, pieces of wood were sectioned, either by hand or by means of a wood-cutting microtome, and both before and after staining were examined and drawn.

Many stains were tried in the course of the microscopic work, but eventually it was decided that the most useful were iodine, chlorzinc-iodine, Mäule's(14) and Cartwright's(5). The most generally satisfactory was the last named because, besides being permanent and demonstrating the fungal hyphae very distinctly, it had the additional advantage of tending to differentiate—using Mäule's stain as a criterion of comparison—between cell walls which gave a lignin reaction and those which gave a cellulose reaction, though it must be admitted that considerable experience in the use of the stain was necessary before one could be satisfied on this point. The unreliability of lignin determination by staining methods is well known, hence, in all cases of doubt Mäule's stain was used, because in the opinion of investigators such as Crocker(6), Harlow(7) and Phillips(17), etc., it is the most satisfactory. The microscope drawings were done with the aid of a Leitz projection apparatus.

In writing up this part of the work, the matter was considered under the respective headings "The effect of the fungus on the timber" and "The effect of the timber on the fungus", though considerable overlapping was unavoidable.

(*a*) *Effect of the fungus on the timber.*

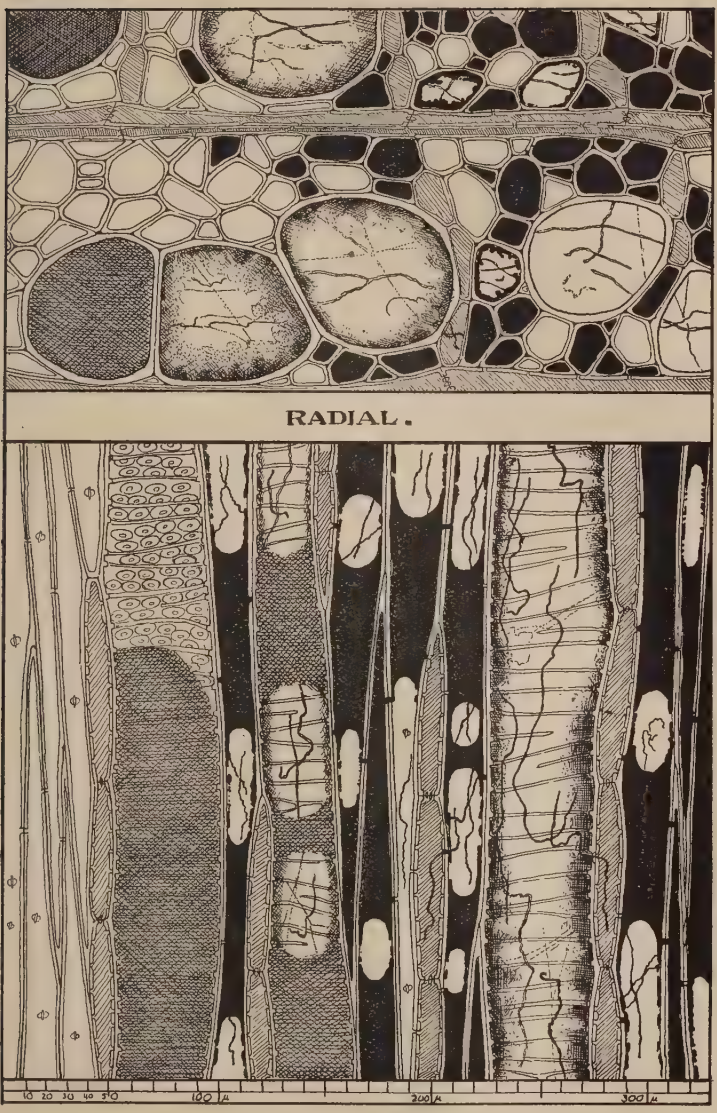
(i) *The discoloured wood.* The sound wood hardly comes into this at all, so it will be well to start with the discoloured wood (see Plate I, fig. 4, B, C). This is about 1 cm. wide and is seen to consist of two regions:

(1) A peripheral zone about 5 mm. wide, dark red-brown and bordering on the sound wood. This type of wood will be referred to subsequently as "D2".

(2) The discoloured wood itself which, being very variable in width, can hardly be described as a "zone". This is of the same general colour as the D2 but less deep in tone; it will be referred to as "D1".

In both, the discoloration is largely consequent on the deep colour of the cell walls, those of the rays and wood parenchyma being yellow while those of the vessels and tracheids are red-brown. In addition to the deep colour of the walls, however, the D2 wood shows the phenomenon of occlusion of both vessels and tracheids by dark brown infiltrations. These have the superficial appearance and give the same staining reactions as the substances described by certain previous workers under the somewhat indeterminate heading of "wound gum". An interesting feature of these products is that when stained with Cartwright's stain, the products in the vessels stain blue (? cellulose complex) while those in the tracheids stain red (? lignin complex).

In the outermost half of the D2 region only the vessels are filled with these products, but in the innermost half the tracheids also are



Text-fig. 4. Transverse and radial sections through the timber in the wound-gum region. The red-stained infiltration products in the tracheids are in full black, while the blue-stained products in vessels are cross-hatched.

filled; in fact, the massing of the products in this region is so abundant that practically every tracheid is filled with them. The products, though commonly found in vessels and tracheids, are comparatively infrequent in rays and parenchyma. Text-fig. 4 shows the transverse and radial appearance of this region of the wood, the blue-staining products in the vessels are cross-hatched, while the red-staining products in the tracheids are in full black. From the radial section it will be seen that the products are not continuous throughout the whole length of the tracheid but are interrupted at irregular intervals by spaces. This produces in transverse section the erroneous effect that a considerable number of the tracheids is empty. In certain vessels products are found to be adhering round the walls, while the centre is devoid of such products; these vessels invariably contain hyphae, and it is suggested that the products are probably being digested by the fungus.

The D1 wood, though having the coloured walls, does not show the filling up of the cells to any extent; occasionally cells are so filled but it is comparatively rare.

The discoloured wood of the root is essentially similar to that of the stem, except that there is less evident distinction between the D1 and D2 types of wood owing to the fact that all the cells of the D1 region of the root show a higher proportion of infiltration.

Though this discoloration may be taken to represent "incipient decay" it must, from the decay point of view, be taken as an indication rather than a fact, as the most careful examination failed to reveal any structural disintegration of the timber in the discoloured region.

(ii) *The diseased wood.* The diseased wood is delimited from the discoloured wood by the black line, as shown in Plate I, fig. 4, at C. Behind this line the wood is light in colour, crumbly in texture, and has, in fact, all the superficial characters of diseased wood. Microscopic examination, however, shows that disintegration is not a direct function of the black line itself, for actual disintegration commences about 5 mm. behind the black line. This is in agreement with the observations of Hiley ((10), p. 156) on the black line of *Armillaria mellea*, where he says "when looked at with the microscope it is remarkable how little difference can be seen in the wood on the two sides of the black line. . . nevertheless at some distance behind the black line marked delignification does take place". Besides the black line which is found on the edge of the diseased wood, other apparently similar lines occur scattered indiscriminately throughout the older parts of the diseased wood; as these black lines consist entirely of hyphae they will be discussed later.

The diseased wood some few millimetres behind the black line shows the first stage of decay. This decay is always more marked on

the autumn than on the spring-wood side of the annual rings. The large vessels of the spring wood appear to be unaffected; they remain intact, show no change of structure and no difference in their reaction to stains. The tracheids of the spring wood, however, are beginning to show some sign of change, their walls are thinner and less rigid than those of the sound wood, though they continue to give a lignin reaction. Below the ring, decay is more advanced; the walls of the vessels are still unaffected, but the tracheid walls have become much thinner, have lost their rigid structure and appear wavy and fragile; often there seems to be little but middle lamella left. They show evidence of considerable delignification.

In both spring and autumn wood, the rays and wood parenchyma remain apparently quite unaffected.

In very badly diseased timber, farther back from the line, the above state of affairs is emphasised; vessels, rays and wood parenchyma still show no sign of disintegration, but the tracheids of the spring wood have now reached the stage described above for the autumn tracheids, while the tracheids of the autumn wood here are completely disorganised, the walls have broken down completely and only a few scattered fragments of the middle lamella are left.

By the use of suitable stains, the course of the disintegration can be suggested. Both Mäule's and Cartwright's show when the wood fails to give a lignin reaction—the former by the absence of colour and the latter by the presence of a blue colour. It is difficult to state that the absence of the lignin reaction indicates that the delignified wall was reduced to cellulose as no cellulose indicators (such as chlor-zinc-iodine) gave a consistently positive result. The experimental use of the stains on other timbers, however, tended to indicate the probability that it was so, and this has been tentatively assumed.

Stages in the disintegration of the tracheids can be said to occur as follows:

The first stage is the appearance of delignified spots in the wall. With Mäule's stain the effect is as if a piece of the wall has been "bitten out", but Cartwright's stain shows that there is still wall substance in these spots, as, with this, they stain blue. This sort of thing develops until large parts of the wall become delignified, and often it is only at the corners that any sign of lignification remains. Eventually the whole of the wall becomes delignified and at the same time seems to be much thinner, *i.e.* it appears to collapse simultaneously with the disappearance of the lignin. At this stage the wall may lose its rigidity and become wavy or even broken. The last stage of wall disintegration is that only the middle lamella is left and finally the tracheids disappear entirely leaving an empty space surrounded by the non-disintegrated elements.

The skeleton formed by the vessels, rays and wood parenchyma

when the tracheids have disappeared, ensures that lime wood decayed by *Ustulina* always retains a certain stability even when the specific gravity is reduced to about 0·2 and the wood crumbles readily in the fingers. An example of the skeleton effect produced in a very badly decayed piece of timber is illustrated in Text-fig. 5. This also illustrates the relative frequency of fungal hyphae at this stage of decay.

(*b*) *Distribution of the fungus mycelium in the timber.*

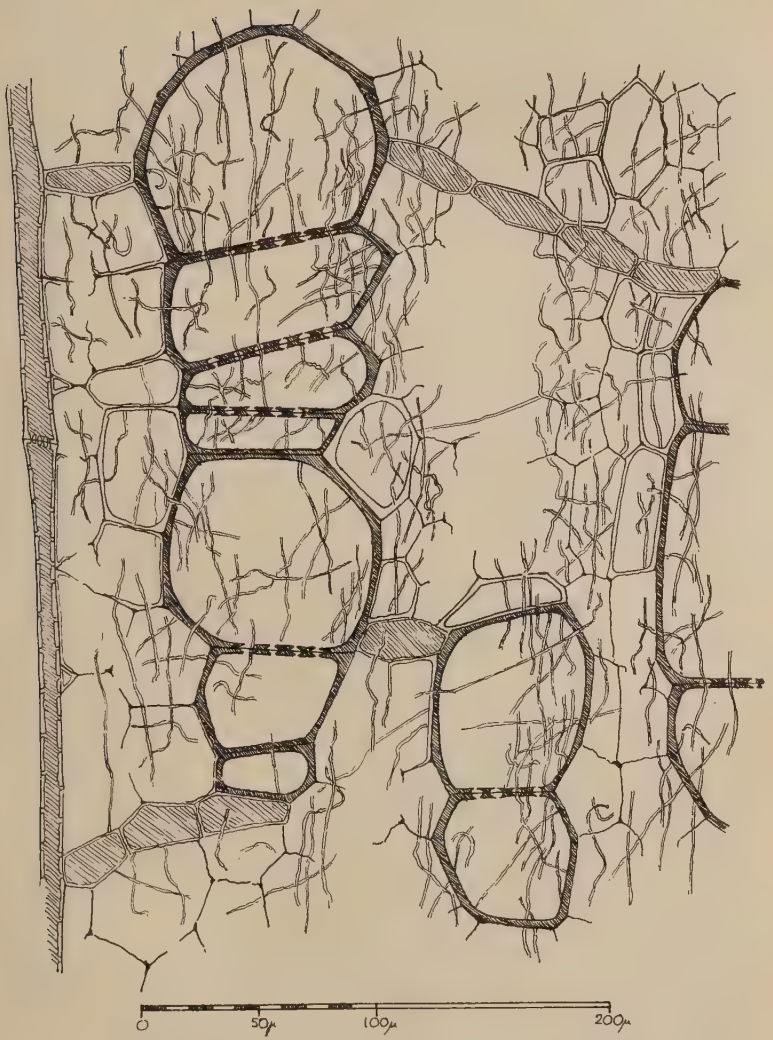
The mycelium penetrates the whole of the diseased and the discoloured areas. In spite of the fact that no cultures were obtained from borings taken from the discoloured wood, microscopic examination reveals the presence of hyphae in that wood. Taking the strip of wood (Plate I) in the same order as before, it is found that hyphae are first seen in the sound wood outside the discoloured area. For about 5 mm. beyond the outer margin of the discoloured wood, the hyphae are fairly abundant—though not as numerous as in the discoloured wood itself; and some—relatively few—hyphae are found to extend as far as 10 mm. beyond the margin. Unless otherwise stated, all the hyphae are narrow—about 1 μ in diameter.

In the D2 zone the hyphae are fairly abundant; there are approximately three hyphae in each vessel and they are rather less frequent in the tracheids. It has been stated before that in the outer part of D2 it was only the vessels that showed decomposition products, and this would appear to be correlated with the distribution of the hyphae. In the innermost part of this region, where the tracheids also showed infiltration, hyphae are more numerous in the tracheids, but where the infiltration is very dense they are either absent or indistinguishable. It was noticed that all vessels which had the products only round the margin of the cell invariably contained hyphae.

The D1 region contained relatively fewer hyphae; approximately half the vessels and rather fewer of the tracheids contain about one or two hyphae each. It would appear, therefore, that there is a slightly increased development of hyphae in the outer region of the D2 margin of the discoloured wood. In both regions hyphae were occasionally found in the rays and parenchyma.

The next region is the black line. It is usually a few cells wide, and the cells comprising it are densely filled with black contents so that the whole line appears as an amorphous mass (Brooks(2), p. 160). In thin sections, however, and particularly on the edge of the line, the "tylose" origin of these lines, as commented on by several investigators, is very obvious. This appearance is illustrated by Small ((20), Plate II, fig. 9), by Hiley ((10), pp. 155 and 157) in connection with *Armillaria* on larch, and by Campbell ((3), Plate III, figs. 1, 2 and 3).

In the black line no hyphae of the ordinary type could be dis-



Text-fig. 5. A transverse section of a very diseased part of the timber (explanation in the text).

tinguished owing to the dense massing of the black substance. On the side of the line which is towards the discoloured wood, however, large septate hyphae—about 4 μ in diameter—appear to grow out from the black line substance, and they extend vertically up the vessels, tracheids and parenchyma for a distance of about 0·5 mm. and for approximately the same distance along the rays. These hyphae are all filled with a dark-coloured substance in the part which is nearest the line, but this discoloration gradually decreases towards the more distal parts, and the ends of the hyphae are hyaline. This state of affairs—which does not appear to have been mentioned by previous investigators—is illustrated in Text-fig. 6 which shows the transverse appearance, and particularly well in Text-fig. 7 which shows the radial appearance of the timber.

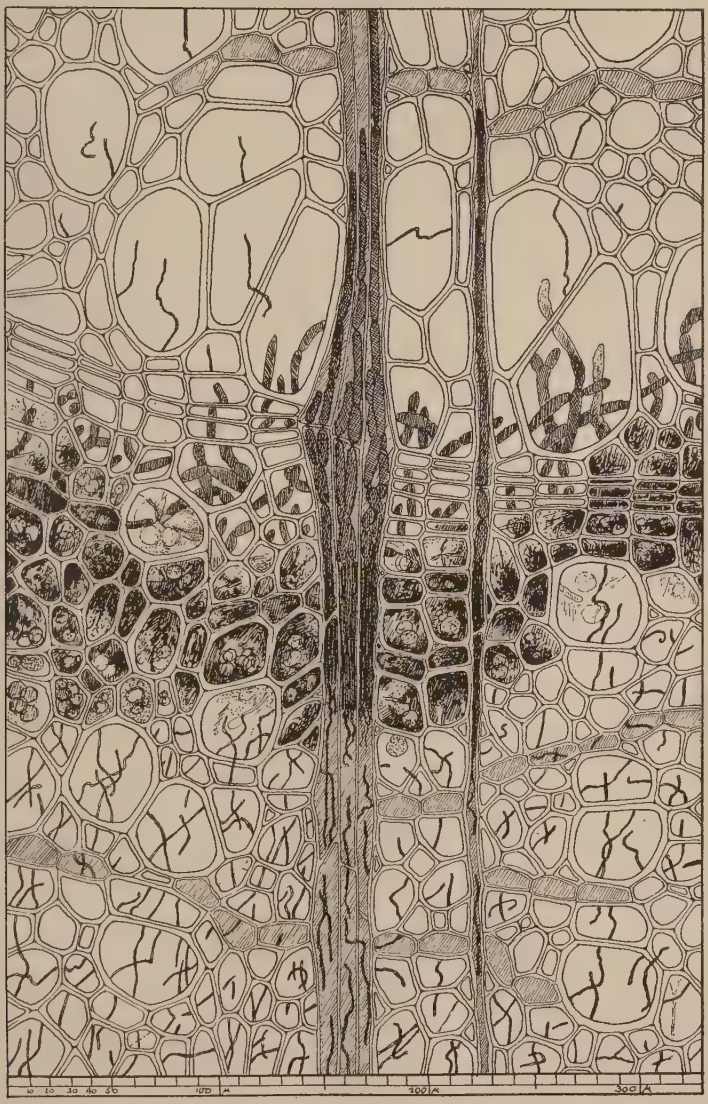
In the diseased wood behind the line, hyphae are present in large numbers; practically all the cells contain them, and sometimes the cells are literally packed with hyphae. These are all of the narrow type. Even here decay is, to some extent, localised; there may be regions where decay is slight with comparatively few hyphae, and other regions not necessarily nearer the original infection—where decay is very advanced and the hyphae extremely numerous. This type of vigorous decay may occur over a region several inches deep, but in the much older parts, where the wood is completely rotten, and has been so for some considerable time, hyphae are relatively infrequent.

Black lines also occur indiscriminately throughout the diseased wood, but, in lines which are not situated at the growing margin of the mycelium, *i.e.* at the edge where the diseased wood borders on the discoloured wood—the line merely shows the usual characteristic appearance, and there is no evidence of the above-mentioned large hyphae. Small hyphae, also, are often much less numerous in the cells associated with the black lines which are situated in the "older" parts of the decayed timber.

Previous workers have suggested that the black line is intimately connected with the process of timber decay, but, up to the present, no adequate account of the significance of the line in this connection has been produced, and I am carrying out investigations on this subject.

(*c*) *Hyphal penetration.*

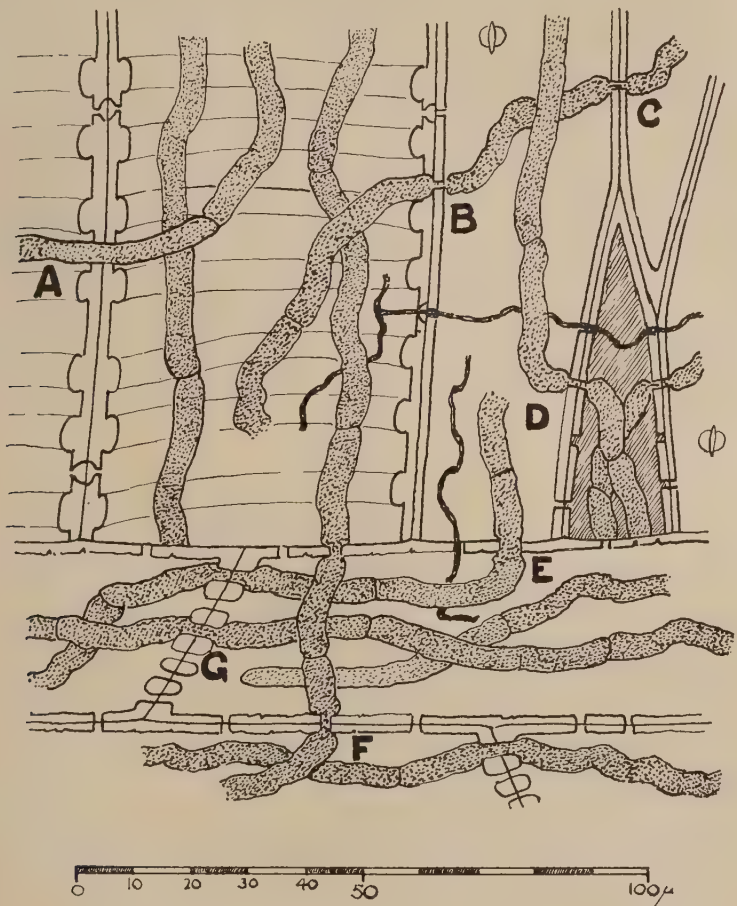
In general, penetration always seems to be by means of the pits; the presence of bore holes was never detected. Nutman (15) found that, in wood subjected to the action of *Polyporus hispidus* for four months, penetration was always by means of pits; and that later penetration of vessels, rays and wood parenchyma (except in the wall bordering on the fibres) was also by means of the pits, but the fibres showed extensive penetration by bore holes.



Text-fig. 6. A transverse section of the junction between the diseased and the discoloured wood, showing the black line and the relative distribution of the hyphae.

Text-fig. 7. A longitudinal section through the same region as shown in Fig. 6.

The 1 μ hyphae were about the same size as the pits and went straight through without apparent alteration. The larger hyphae, on the other hand, were sometimes constricted when they passed



Text-fig. 8. Examples of hyphal penetration (explanation in the text).

through a pit and sometimes not, according to circumstances. Text-fig. 8 shows examples of the various types of penetration.

It will be seen that when the larger hyphae pass from vessel to vessel by means of the bordered pits, the border seems to be dissolved

away and, the pit then being about the same size as the hypha, the latter passes through without constriction (A). When passing from vessel to tracheid or from vessel to parenchyma the hypha is not constricted when it passes through the vessel wall, but is constricted when passing through the wall of the other element (B). In passing from tracheid to tracheid or from tracheid to parenchyma, definite constriction takes place (C and D). When hyphae are passing through the side walls of the rays the degree of constriction varies with the size of the pits, which themselves vary in diameter (E and F), but when passing through the end walls of the ray cells where the pits are rather large, the constriction is slight (G).

Usually the hyphae, having been constricted when passing through a pit, seem to swell up to their original size on the other side, but in certain comparatively rare instances this is not so, and the hyphae continue on the other side for some considerable distance as "narrow" hyphae. Rarely the hyphae flatten out into a disc before passing through a pit; here the actual penetration is probably of the "peg-outgrowth" type, though this has not been seen. In transverse section, the characteristic features of penetration appear essentially the same but are less easily discernible.

V. Conclusions

From the foregoing it seems reasonable to conclude that *Ustulina vulgaris* is capable of forming a very definite disease of standing lime, and from the evidence it is suggested that this fungus is to be regarded as a wood destroyer producing a white rot of the timber to such an extent that the tree may be completely destroyed and the timber reduced to a state where it has little, if any, commercial value. Speaking generally, the disease can be classified as a "white rot" and appears to belong to that type of white rot which falls into the Group II of Campbell(4), *i.e.* a white rot "in which the cellulose with its associated pentosans is attacked in the early stages and in which the incidence of the attack on lignin and the pentosans not in cellulose is delayed".

This paper deals only with the observational facts of *Ustulina* disease of a certain lime, the results of inoculation experiments and experimental work generally not yet being complete are postponed to a subsequent paper. At the moment, however, it is possible to state that all the evidence up to now tends to confirm and justify the opinion that *Ustulina* must be considered as possessing the potentialities of a pathogen of economic importance.

VI. Summary

1. A diseased lime was investigated with the object of determining the cause of disease. The only fructifications present were those of *Ustulina vulgaris* Tul.

2. The causal organism was isolated and proved to be *Ustulina*; this was confirmed by reinfection and subsequent isolation.

3. The tree was cut into sections and the extent of the disease in the stem and root was established.

4. Microscopic examination showed that the fungus attacked the cell walls of the tracheids, leaving the vessels, rays and parenchyma practically unaffected.

5. The distribution of the fungus mycelium in the timber was determined by microscopic examination and the types of fungal penetration described.

6. It was concluded that *Ustulina* causes a white rot of lime.

I am indebted to my Research Assistant, Miss E. M. Ellis, B.A., B.Sc., for valuable help in connection with this work.

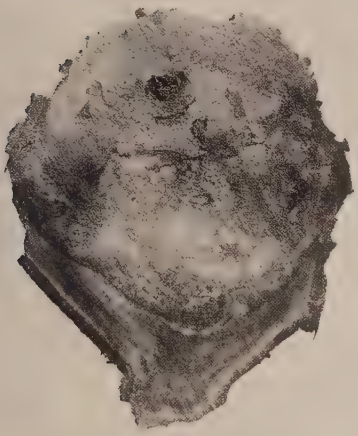
References

(1) Bizzozero, G. *Flora veneta crittog.* I. *Fungi* (1885), p. 199.
(2) Brooks, F. T. "A new disease of plantation rubber caused by *Ustulina zonata*." *New Phytol.* xiv (1915), 152.
(3) Campbell, A. H. "Zone lines in plant tissues. II. The black lines formed by *Armillaria mellea* (Vahl) Quél." *Ann. appl. Biol.* xxi (1934), 1.
(4) Campbell, W. G. "The chemistry of the white rots of wood." *Biochem. J.* xxvi (1932), 1829.
(5) Cartwright, K. St G. "A satisfactory method of staining fungus mycelium in wood sections." *Ann. Bot.* xlii (1929), 412.
(6) Crocker, E. C. "An experimental study of the significance of lignin colour reactions." *J. industr. Engng Chem.* xiii (1921), 625.
(7) Harlow, W. M. "Contributions to the chemistry of the plant cell wall. II. Lignification in the secondary and tertiary layers of the cell walls of wood." *Bull. N.Y. St. Coll. For.* No. 24 (1928).
(8) Hartig, R. *Lehrbuch der Baumkrankheiten* (1882). Berlin.
(9) Heald, F. D. *Manual of Plant Diseases* (1926). New York.
(10) Hiley, W. E. *The Fungal Diseases of the Common Larch* (1919). Oxford.
(11) Hubert, E. E. "The diagnosis of decay in wood." *J. agric. Res.* xxix (1924), 523.
(12) —— *An Outline of Forest Pathology* (1931). New York.
(13) Lind, J. *Danish fungi in Herb. E. Rostrup.* xxii (1913), 334.
(14) Mäule, C. "Das Verhalten verholzer Membranen gegen Kaliumpermanganat, eine Holzreaktion neuer Art. (*Beitr. wiss. Bot.* iv (1901), Stuttgart.) *Bot. Z.* lxxxix (1902), 328.
(15) Nutman, F. J. "Studies of wood-destroying fungi. I. *Polyporus hispidus* Fr." *Ann. appl. Biol.* xvi (1929), 40.
(16) Patouillard, M. "Sur le parasitisme de l'*Ustulina vulgaris*." *Bull. Soc. Path. vég. Fr.* iv (1917), 100.
(17) Phillips, M. "The chemistry of lignin." *Chem. Rev.* xiv (1934), 103.

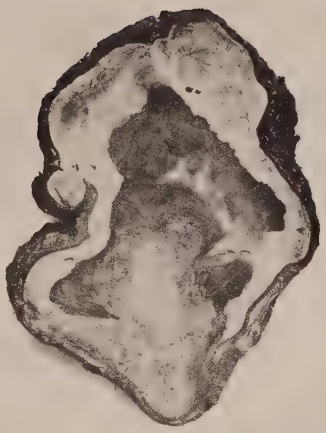
(18) Schrenk, H. von. "A disease of the white ash caused by *Polyporus fraxinophilus*. *Bull. U.S. Bur. Pl. Ind.* No. 32 (1903).
(19) Sharples, A. "*Ustulina zonata*, a fungus affecting *Hevea brasiliensis*." *Bull. Dep. Agric. F.M.S.* No. 25 (1916).
(20) Small, W. "On *Rhizoctonia bataticola* (Taub.) Butler, as a cause of root disease in the tropics." *Trans. Brit. mycol. Soc.* xiii (1928), 40. (*Rev. appl. Mycol.* vii (1928), 604.)
(21) Steinmann, A. "De ziekten en plagen von *Hevea* in Ned.-Ind." *Arch. Druk.-Buitenz.* (1925), p. 24 (*Rev. appl. Mycol.* iv (1925), 701). English summary, *Biol. Abstr.* v (1931), 1038.
(22) Sydow, P. *Mycotheca marchica* (1890). (Herb. Mus. Brit.)
(23) Van Overeem, C. "Über *Ustulina vulgaris* Tul. und *U. zonata* (Lév.) Sacc." *Bull. Jard. bot. Buitenz.* Sér. 3, vi (1924), 256. (*Rev. appl. Mycol.* xx (1925), 90.)
(24) Wehmer, C. "Pilzkrankheiten land- und forstwirtschaftlicher Kulturgewächse in Hannoverschen während des Sommers 1896." *Z. Bakt.* Abt. 2, ii (1896), 796.
(25) Weir, J. R. "Pathological survey of Para rubber tree in Amazon Valley." *Bull. U.S. Dep. Agric.* No. 1380 (1926), p. 13.
(26) Wilkins, W. H. "Studies in the genus *Ustulina* with special reference to parasitism. I. Introduction, survey of previous literature and host index." *Trans. Brit. mycol. Soc.* xviii (1934), 320.

EXPLANATION OF PLATE I

Fig. 1. Transverse appearance of the lowest section of the stem, cut at a height of six feet from ground level.
Fig. 2. Transverse appearance of the first root section, cut at a distance of nine inches from the junction with the trunk.
Fig. 3. A "close-up" view of the superficial mycelium which appeared on the above root section.
Fig. 4. The transverse (left) and radial (right) appearance of a strip of timber cut down the centre of stem section 2 (explanation in the text).



1



2

3

4

HYGROPHORUS WITH DIMORPHOUS BASIDIOSPORES

By E. J. H. CORNER
Botanic Gardens, Singapore

(With 8 Text-figures)

I have found in Malaya two species of *Hygrophorus* with dimorphous basidiospores. Side by side, on the same fruit body, occur large spores on large basidia and small spores on small basidia. The large spores have dense contents and roughly twice the linear measure of the small spores which are hyaline and vacuolate and often with a slightly different shape. The meaning of this dimorphism, which is unknown in any other Basidiomycete, cannot be as great as one would at first suspect and is by no means equivalent to true cryptogamic heterospory. For, in the first place, both species are very similar in all other respects to certain common and well-known European members of this large, unspecialised genus, and unlikely, therefore, to have evolved a new physiological condition. And, in the second place, both kinds of spore invariably occur on the same fruit body, on adjacent hyphae, and all the basidia are tetrasporous and clamped (the small basidia rarely being disporous), so that a sexual or karyokinetic difference can scarcely exist. It is perhaps just the full consequence of a vegetative dimorphism which occurs among the hyphae of the fruit body of these, as in many other agarics: in the primordium, all the hyphae are similar, but some inflate strongly and some hardly at all, and so of the basidial branches, which are initially similar, some inflate strongly to produce the large spores and others but little to produce the small spores. But I have examined only the morphological aspect.

One species, *Hygrophorus firmus*, is known already from Ceylon, where Petch remarked on the dimorphism (4). In Malaya, it varies exceedingly in shape, colour, size and spore characters, surpassing even *Laccaria laccata* or *Omphalia umbellifera*, and, reckoned with its varieties, it is one of our commonest toadstools. The other, which I propose to call *Hygrophorus hypohaemactus* from the rich colour of the hypodermal tissue, is new and probably rare. They differ chiefly in a way which is not infrequent in the genus. In *H. hypohaemactus* the hyphal ends on the surface of the fruit body have mucilaginous walls and their cells are not inflated, whereas in *H. firmus* they have firm, not diffluent, walls and at least over the pileus they are inflated. There is also less dimorphism in the spores and basidia of *H. hypohae-*

mactus, but in colouring, form and hyphal construction they agree. Macroscopically, *H. firmus* is like *H. miniatus*, and illustrations of that species, or Bresadola's of *H. Marchii* (*Iconogr. mycol.*, Firenze, VII, 343), would represent the typical state. *H. hypohaemactus* inclines rather to *H. coccineus*.

In the first part of the paper I have described the structure and development of the fruit body, which offers certain points of interest in the origin of the pileus, the marginal growth of the limb and gills, and the expansion mechanism of the fruit body. I have also included a summary of the bionomical observations which I have made in Singapore on the fruit body of *H. firmus* var. *stratiotes*: they will be published in detail at a later date together with illustrations of the development and shape of the fruit body in both species and varieties.

The structure of the mature fruit body of *Hygrophorus firmus* var. *stratiotes*

The stem. The hyphae are very compact and chiefly of two kinds: either they are strictly longitudinal with inflated cells, 120–1800 × 10–35 μ, or narrow and more or less interwoven with the cells passively extended, 20–200 × 3–5 μ. Both kinds are clamped and the narrow ones are more frequently branched, the branches arising from any part of the cell, generally from the distal half. The contents of the wide hyphae are clear and vacuolate, though sometimes vitreous at the tapered ends of the cells; those of the narrow hyphae are vacuolate and rather smeary-looking, or they are frequently oily throughout, but initially, in the primordium, all the hyphae are similar and the narrow ones begin to acquire their characteristic appearance when the fruit body is about half-developed.

Many intermediates occur between the two kinds, and the one often gives rise to the other. Generally the cells of a hypha are inflated throughout its length or not inflated, but often a few inflated cells may lie between rows of narrow cells, and even the same cell may be inflated at one end only or in the middle, or occasionally in several places, so appearing nodose.

At the surface of the stem the hyphae are all narrow, 3–8 μ, and scarcely inflated. Some of the hyphal ends project obliquely up to 200 μ as narrow filaments with one or two septa and occasionally branched, but they are scattered and there is no palisade of caulocystidia: the terminal and subterminal cells of the hyphae may be slightly inflated, 25–45 × 5–14 μ, especially near the apex of the stem. The hymenium begins abruptly with only a few small tufts of cystidia and sterile basidia preceding it.

The hyphae bordering the hollow of the stem are mostly narrow and not inflated.

The stem is waxy and brittle, owing to this arrangement of the

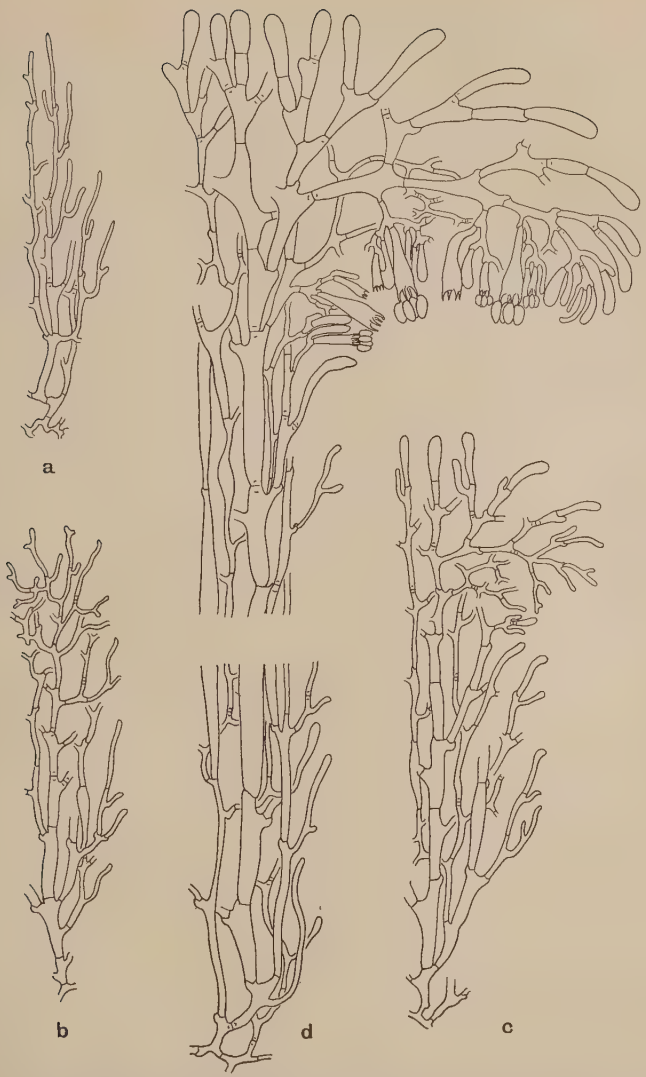


Fig. 1. Diagrams of characteristic hyphae from successive stages in the development of the fruit body of *H. firmus*: *a*, the primordial shaft; *b*, the primordial shaft on development of the pileus; *c*, with primordial limb and incipient hymenium; *d*, the mature fruit body.

hyphae, and snaps easily under the weight of the pileus when displaced from the vertical.

The pileus. The structure is like that of the stem, but the inflated hyphae are frequently 40 μ wide and rarely so long (up to 600 μ). At the surface the hyphae are all inflated. Over the centre their ends form an irregular pile of simple obtuse filaments, two to four cells long, and projecting freely or in groups up to 300 μ high, which gives the scurfy appearance to the disc: their cells are 60–200 × 9–25 μ, and rarely branched. Over the limb the hyphal ends are radiating, adpressed and rather narrower so that the pile is scarcely recognisable and the surface is inoderm, while near the margin their cells are only 20–60 × 7–15 μ and pass conformably into the hymenium.

The trama. The structure is like that of the pileus, but most of the hyphae are inflated with shorter cells, up to 200 μ long, but as wide as in the pileus. The trama and the tissue of the pileus immediately above the gills are hygrophanous with water, or very dilute mucilage, between the hyphae.

The subhymenium. This tissue is also hygrophanous. It is loosely plectenchymatous, being composed of narrow hyphae with cells 8–35 × 2–4 μ, not inflated, but pulled apart through the intercalary growth of the hymenium.

The hymenium. The basidia are dimorphic. The large basidia arise deeply in the subhymenium and terminate some distance beyond the general level of the small basidia; the large spores project well beyond the small spores. Both kinds of basidium are borne on the same hyphae, the large basidia being derived from deep-seated laterals and the small basidia from the superficial laterals; intermediates are rare. The small basidia far outnumber the large basidia which are dispersed evenly without bunching, though they are generally absent from the first-formed parts of the hymenium at the junction of the gills with the stem. As the young pileus is expanding, the basidia mature acropetally from the stem apex to the margin of the limb and obliquely outward down the gill to its edge, but very soon the gills become aequihymeniiferous, and large and small spores are shed together. There are no pleurocystidia.

The gill edge. The construction varies but the edge is always sterile. The simplest condition shows a narrow strip of cheilocystidia, formed from the modified ends of the down-growing tramal hyphae. Transitions between the cheilocystidia and small basidia are frequent, as clavate cells with abortive sterigmata and even rudimentary spores. More complicated conditions show the ends of the tramal hyphae, 3–5 μ wide, far exceeding the hymenium and matted in a loose plectenchyma, while their ends may inflate, 6–10 μ, and appear in surface view as decumbent or immersed cystidia.

The colour. As is general in *Hygrophorus*, the brilliant red or yellow

(and its modifications in the other varieties of *H. firmus*) is due to a pigment dissolved in the cell sap of the superficial hyphae. The internal hyphae and those of the hymenium are colourless.

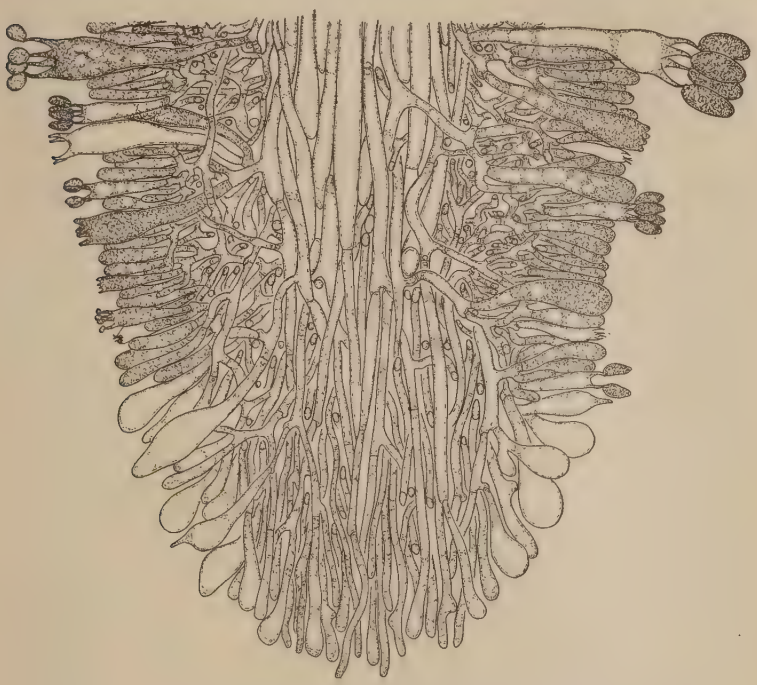


Fig. 2. The edge of a gill of *H. firmus* on cessation of downgrowth; ×400.

The development of the fruit body of *Hygrophorus firmus* var. *stratiotes*

Macroscopic features. Development is gymnocarpic and direct, with exogenous pileus. A conical primordial shaft, 0·5–3·5 × 1–2 mm., is first developed; it is initially colourless but soon becomes pale orange save at the tip. A small swelling, 1–2·5 mm. wide, then forms at the tip through outgrowth on all sides. Presently the outgrowth increases in an equatorial belt and the limb develops. Through epinasty the limb becomes convex with the margin slightly incurved. All the while, the part below the swelling is enlarging, elongating and raising the pileus, to become the stem; it soon colours scarlet, though not as deeply as the pileus. The primary gills develop almost as soon as

the pileus, and the secondaries and higher ranks are intercalated regularly at the margin. The pileus begins to expand before the stem is fully elongated. The limb straightens, becomes horizontal and finally is thrust upward by the expansion of the gills which renders the pileus concave or infundibuliform. The stem soon becomes hollow because the internal tissue is disrupted on expansion of the peripheral, and the excessive growth of the gills may disrupt the central tissue of the pileus and cause the fruit body to be pervious to the base.

Microscopic development

The primordial shaft. Composed of longitudinal interwoven hyphae, the primordial shaft enlarges by apical growth and acropetal inflation of the cells. The hyphal tips, 1·5–3 μ wide (mostly 2–2·5 μ), are rounded and obtuse with the apical cells 12–55 μ long. They grow monopodially and often branch by lobing from the apical cell without concomitant septation, or from the subterminal cells, which are mostly 12–30 μ long on delimitation. The direction of growth varies so that the hyphae are interwoven, but as a whole the apex of the primordium grows away from the substratum. The enlargement of the cells begins at the base of the primordium, which is therefore conical; when the primordium is barely 0·5 mm. high, the hyphae at the base are beginning to inflate, and when 0·5–1 mm. high, the cells in the basal third measure 20–60 × 4–10 μ. The hyphae on the outside of the growing point of the primordium gradually cease growing: they are left behind on the surface and their ends either remain unmodified, adpressed or slightly projecting, or they may inflate slightly, 5–14 μ wide, as already described: but they are never abundant and do not branch regularly or profusely so that neither a pile nor a palisade is constructed. The tissue of the primordium is hygrophanous throughout, water filling the interstices between the hyphae and rendering the whole translucent.

This is the general organisation of the primordial shaft in the higher fungi, but it has not previously been described in detail for a gymnocarpic agaric.

The pileus initial. After a short interval, 36–60 hours, from the origin of the primordium, when it is 1–3 mm. long, apical growth is checked. The terminal cells of the longitudinal hyphae at the tip of the primordium begin to inflate, becoming narrowly clavate, 3–5 μ wide. From their subterminal cells numerous laterals arise and, growing to the surface by devious routes from various depths, are checked and branch again in their turn. The apex of the primordial shaft thus swells into a small head composed of narrow, 1·5–3 μ, densely interwoven hyphae, the ends of which are excrescent from the whole surface except over the original apex of the shaft where a dead space has formed. In this dead space the hyphal ends arrange

themselves in a pile which, together with the underlying interwoven tissue, will become the *disc*, or centre, of the pileus. The dead space extends centrifugally, and simultaneously, the outgrowth from the lower side of the "head" is checked in a zone round the stem apex, and this zone spreads upward over the side of the "head", except along certain radial paths which become the paths of outgrowth of the primary gills. Outgrowth from the head of the primordium is thus checked from above downward and below upward but continues in an equatorial zone as the marginal growing region of the pileus. The form factors begin to play, as usual, in a region where an active and regular outgrowth has been established.

The marginal growth of the pileus. As the hyphal ends grow out in an equatorial zone round the head of the primordial shaft, they build up the limb. This zone becomes the margin of the limb, the growth of which is monopodial like that of the primordial shaft, but the tissue of the limb, which it constructs, is dorsiventral and the margin becomes incurved. This epinasty is due partly to the dorsiventral structure and partly to a directive growth of the hyphal tips. One can consider the limb as a corticated, multifilamentous, centrifugal and fan-shaped soma, the cortex on the upper side being the sterile pile, that on the lower side being the hymenium, and the wide intervening medulla forming the flesh. The hyphal ends in the marginal growing region behave like those at the apex of the primordial shaft, but those which drop behind are modified according as they lie on the upper, outer or lower, inner side (Fig. 3). If they lie to the outside, their terminal cells enlarge, becoming clavate, and eventually inflated up to 25 μ wide: they become coloured, and branch sparingly from the coloured subterminal cells, and form the pile on the pileus: their proximal parts contribute to the medulla of the limb along with the subterminal cells of the main longitudinal hyphae from the margin. If they lie to the inside, their terminal cells enlarge into basidia and are unpigmented. The terminal cells of the upper sterile cortex enlarge sooner and to a greater extent than the first formed basidia in the hymenium (which are undergoing meiosis), and thus the margin of the limb is pressed down and in, toward the stem, as a mechanical effect of the growth of the pile. But the hyphal tips at the margin tend to grow toward the stem by a curvature independent of tissue pressures and determined by some intrinsic property of the apical cells (Fig. 3). There is no evidence that the hyphal tips are geotropic, although they may be negatively phototropic.

The pileus. As already explained, a close pile is built up over the centre of the pileus from the ends of the longitudinal hyphae of the primordial shaft and their laterals. A similar pile is built over the limb, but as the limb extends, the hyphae of the pile do not inflate or branch as much, but are more or less decumbent. The hyphae

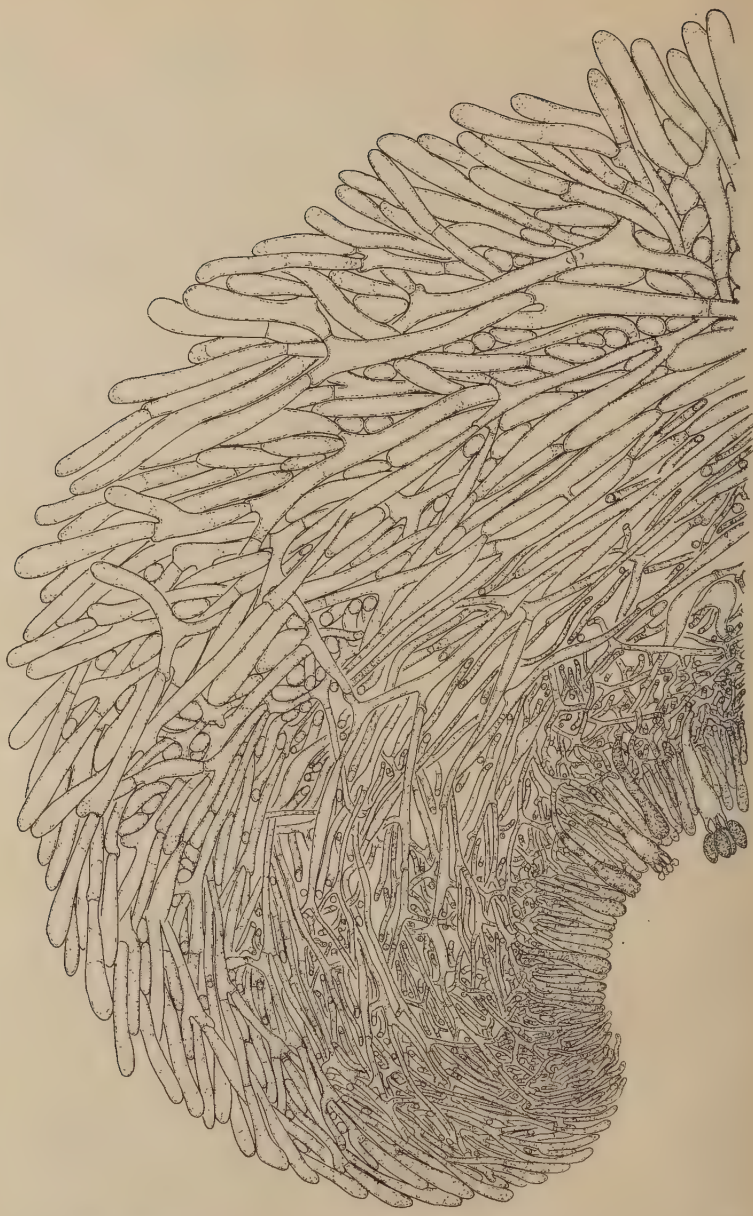


Fig. 3. A radial section of the margin of the limb in the primordial pileus of *H. firmus*; × 250.

of the pile are deeply pigmented and the unexpanded or partly expanded pileus appears like scarlet velvet. As the medulla extends the pile is disrupted into scurfy particles, becoming almost unrecognisable in mature pilei, and the colour is diluted and gradually fades. In some specimens the decumbent hyphae on the upper side of the limb scarcely branch at all and the limb appears inoderm without a pile.

The gills. As in *Collybia apalosarca* (2), the gills develop as ridges along radial paths on the under side of the limb where the outgrowth from the primordial head is not checked. Along these paths, which extend radially with the growth of the limb, the hyphae grow monopodially, as they do at the margin of the limb. The gills are thus formed by the outgrowth of hyphae. This is clear when the tramal hyphae are excrescent to form a loose plectenchyma along the gill edge (Fig. 2). And as the primary gills diverge centrifugally, keeping a constant width, so the secondaries and, in their turn, the higher ranks are intercalated. At the sides of the gill edges the apical growth of the hyphae slows down; their apices bulge out unilaterally at right angles to the tramal hyphae and develop into basidia. The first basidium is generally large. Laterals arise from the subterminal cells and, growing up in the same direction, generally terminate in large basidia: laterals arise from their subterminal cells, and growing up to the level of the large basidia cut off one or two short, subhymenial cells and terminate in small basidia. Sympodial branching then continues profusely, the deep-seated laterals generally becoming large basidia, the more superficial ones small basidia. Thus the level of the hymenium is built out into the gill spaces on a relatively thick subhymenium, and one finds the large basidia scattered among the crowds of small basidia. The large basidia originate in the same way as the pleurocystidia of *C. apalosarca*, and their stalks traverse the subhymenium. On cessation of growth the hyphal ends along the gill edge enlarge into the cheilocystidia.

The basidia and spores. On account of their size the large basidia are convenient objects for study (Fig. 4). One can distinguish three main processes: the accumulation of cytoplasm in the basidium, the vacuolation of the basidium driving the cytoplasm into the sterigmata and spores, and, concurrently, the stretching and stiffening of the cell wall fixes the shape. The basidium is full sized before the sterigmata develop, and the sterigmata before the spores appear; the maximum of the grand period comes toward the end of the first stage at the apex of the basidium with a secondary maximum in the spores.

The basidia enlarge through the accumulation of cytoplasm. While they are slender hyphal ends, they are finely vacuolate and transparent but, as they grow, numerous anabolites are precipitated as reserve substances to be lodged in the spores, and when they are full-sized

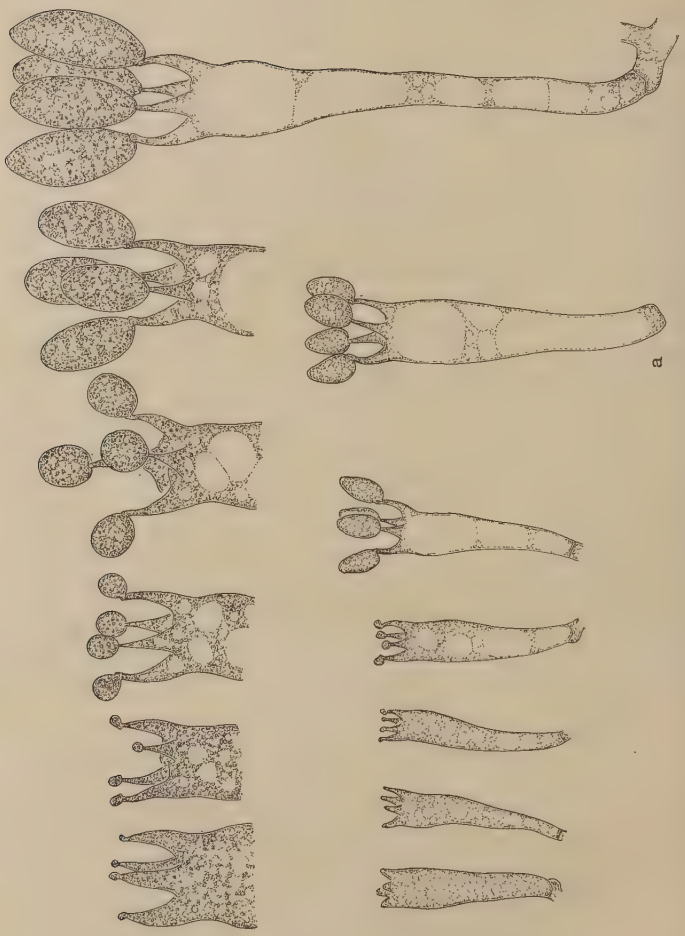


Fig. 4. Stages in the development of large and small basidia of *H. firmus* var. *stratiotes*; *a*, an intermediate basidium; × 1000.

and cut off by a septum their contents throughout are densely granular and guttate. The wall of the basidium stiffens acropetally leaving four thin spots at the apex, and this leads to the second stage. Vacuoles appear at the base of the basidium as a few small spaces in the cytoplasm, then in the middle of the basidium, and as they enlarge they press upon the denser cytoplasm, the pressure being transmitted to the four weak spots at the apex, and the sterigmata are pushed out as *blunt* processes: the internal pressure of the basidium now becomes a simple turgor pressure. The walls of the sterigmata are at first elastic throughout but soon begin to stiffen acropetally and the sterigmata taper to an acute apex: this begins the third stage. The spores arise as minute lateral swellings on the abaxial side of the sterigmata just below their tips, at a point where the wall has not yet stiffened. The vacuoles in the basidium continue to enlarge, forcing the granular cytoplasm into the spore rudiments which swell into spherical bodies, indicating that the spore wall is growing uniformly. The spore wall then begins to stiffen acropetally and the distal end of the spore is forced into a blunt cone, like the sterigma. The basidium and its appendages can then enlarge no further although the turgor pressure continues to rise. This instability leads to the discharge of the spores, which has been fully investigated by Buller(1). The cell wall, in a state of increasing tension, finally gives way at the weakest point, at the necks of the sterigmata, and the basidiospores are violently shot off with a drop of escaped fluid.

How the cytoplasm is forced into the spores can readily be gathered from Fig. 4. The vacuoles must be special structures, for there is no general hydration of the cell contents and their walls must be strong enough to press upon the non-vacuolated cytoplasm. The shapes of the basidium, sterigmata and spores are clearly determined by the properties of the cell wall, especially the extent to which it can be stretched locally. Those parts of the wall where the sterigmata and spores emerge, as well as that which finally gives way, may of course be weakened after stiffening, but it is simpler to construe them as direct steps in the continuous development of the organ: the problem is why the sterigmata and spores are blown out only in certain places.

It is not obvious how the spores are discharged successively, as Buller describes. One would expect the contents of the basidium to escape through the hole in the sterigma as soon as the first spore was shot off; either the hole is too minute or it contracts elastically.

The small basidia and their appendages develop in a similar way; their contents are never coarsely granular or guttulate. The intermediate basidia, which are scarce, develop at intermediate depths in the subhymenium and bear spores of intermediate size. I have never seen small and large spores on the same basidium.

The motor mechanism of the fruit body

One must distinguish between the chief motor mechanism which expands the fruit body and the expansion of the palisades which merely sets up local tissue pressures. The chief motor mechanism lies in the medullary hyphae which gradually inflate acropetally in a grand period of growth in the stem, pileus, and trama, as I have described in *Collybia apalosarca*. Inflation in the primordium is inconsiderable until the pileus is initiated: the medullary hyphae of the stem then rapidly inflate carrying up the rudimentary pileus, the central medullary tissue of which also begins slowly to inflate. The wave of inflation passes from the stem into the pileus, radially to its margin and obliquely outward and downward in the trama of the gills: the stem is nearly fully expanded when the pileus is about half-expanded. The cells in the primordial shaft average 20–2·5 μ on delimitation; they straightway begin to inflate slowly and in the mature stem they average 400 × 20 μ, elongating about twenty times; this proportion corresponds with the macroscopic growth of the stem: the primordial shaft reaches an average height of 2 mm. and the stem of the full-grown fruit body averages 5 cm.

Not all the medullary hyphae inflate. Very few inflate in the core of the primordial shaft, which is thus disrupted to form the hollow of the stem. The inflating hyphae are dispersed evenly through the medulla of the pileus and trama, which do not become hollow.

The inflation of the palisade hyphae does not take place in such uniform sequence. It is generally basipetal, beginning in the apical cell, soon after it has dropped behind the growing margin, and extending through two to four subterminal cells. The terminal cells of the scattered cortical filaments on the stem, the cells of the pile on the pileus, and the basidia all begin to inflate before their corresponding medullary hyphae, and are often nearly fully inflated before any appreciable internal enlargement has occurred.

Whereas the development of the stem is really indirect (a period of apical growth as a primordial shaft being followed by a distinct period of inflation), the limb and gills develop directly, inflation of the cells following closely on delimitation. The limb is at first convex with slightly incurved margin because, as already explained, the hyphae of the pile inflate more rapidly and to a greater extent than the hymenial hyphae. The limb then straightens centrifugally through the inflation of its medullary hyphae and, finally, owing to the intercalary growth of the hymenium and inflation of the gills, it may be thrust upward, becoming concave and the pileus more or less infundibuliform. The pileus mechanism is similar to, but the inverse of, the apothecial mechanism (3).

The fruit body of *Hygrophorus hypohaemactus*

Apart from slight differences in the spores, basidia and cystidia, the fruit body of *H. hypohaemactus* is very like that of *H. firmus*: it is gymnocarpic with exogenous pileus, has both inflated and uninflated medullary hyphae, a distinct pile at least over the centre of the pileus, no pile or palisade on the stem, a sterile gill edge, and the pigment in the cell sap. It differs as follows:

Fig. 5. Part of a longitudinal section of the gill of *H. hypohaemactus*, showing the "pseudocystidia"; × 500.

(1) The hyphae of the pile do not inflate, being 2–7 μ wide in mature fruit bodies, but their walls become very mucilaginous. They are sparingly branched, clamped and with simple ends, and are more or less perpendicular to the surface over the disc and decumbent over the limb. The thick grey mucilage, derived from their walls, becomes so copious in wet weather that it swells beyond the limits of the pileus in dentate and appendicular processes.

(2) The superficial hyphae of the stem also become mucilaginous and are not inflated (2–5 μ wide).

(3) The subhymenial hyphae have thin mucilaginous walls and

are not inflated (2–5 μ wide), so that the subhymenium is subgelatinous and rather thick (*ca.* 50 μ at the base of the gills, 10–20 μ near the edge of the gills, and *ca.* 40 μ on the sides).

(4) Some of the laterals of the tramal hyphae do not contribute to the hymenium with clusters of basidia but lie obliquely disposed as elongate fusiform cells with densely granular oleaginous contents and simple, rarely furcate, obtuse ends. They are either wholly embedded, passing from the trama to the subhymenium, or they project up to 50 μ beyond the hymenium into the gill space or from the edge. They are straight or sinuous, simple or once or twice branched, aseptate, thin-walled, 50–600 × 4–16 μ, × 3–6 μ at the apex, and they look like tramal cystidia. The shorter ones may arise from the subhymenial hyphae and appear as true cystidia in the hymenium. In some fruit bodies they are much more abundant than in others, and owing to their varied origin and disposition they can hardly be called pleurocystidia.

The size of the fruit body

The fruit body varies greatly in size in the varieties of *H. firmus*, from 5 mm. to 17 cm. high, and, as I have shown in connection with *Collybia apalosarca*, the problem is to determine whether this variation is due to differences in the amount of inflation or of apical growth of the hyphae. As in *C. apalosarca*, I have analysed a sufficient number of fruit bodies to show, I think, that it is mainly due to differences in apical growth, since the average amount of inflation is roughly the same. Error is, of course, possible in this method of averaging and extrapolating. Only a few cells are measured in the middle section of the stem, midway between apex and base, and these are assumed to indicate the degree of inflation of the whole fruit body. Fortunately the number of gill ranks gives an independent and simple check on the state of the pileus; this indicates that the pilei of those varieties with small fruit bodies are juvenescent. Also, in the same fruit body, the cells vary greatly in their degree of inflation, and owing to the practical difficulty of tracing the longer cells, the shorter are liable to be picked for measurement. To avoid choosing, I seize upon the septa, measuring the cell on each side of it and then pass to the next obvious septum and so on, finally taking the average of fifty. Nevertheless, the results from both *Hygrophorus firmus* and *H. hypohaemactus* are consistent enough to prove that one is not far from the truth. The fruit bodies of varieties *sericeus*, *minimus* and *gracillimus* may be taken as juvenescent compared with the typical fruit body of *H. firmus* var. *militaris*, and likewise those of *H. hypohaemactus*, but those of the varieties *longipes* and *pachyphyllus* are clearly overgrowths (the average length of an inflated cell from the stem is 400 μ). But the variations in size between fruit bodies of the same

troop, *i.e.* contemporary from the same mycelium, are as often due to differences in apical growth as inflation.

Table A. *Showing the relation between the size of stem and inflation of the cells in* H. firmus

	Stem size in mm.		Stem-length ratios	Average cell length from middle section of stem	Ratios of average cell lengths	Cell extremes	
	Length	Width in middle					
H. firmus var. *militaris*	53	2·5	1	460	1	92–1513	One tuft
	50	2·5	0·94	429	0·9	150–825	
H. firmus var. *stratiotes*	86	4	1·6	563	1·2	170–1170	One tuft
	75	5	1·4	584	1·3	200–1750	
H. firmus var. *gracillimus*	17	1	0·3	398	0·9	150–750	One tuft
	15	1	0·3	374	0·8	120–720	
	11	1	0·2	410	0·9	100–850	
	12	1	0·2	325	0·7	120–600	
H. firmus var. *stenophyllus*	40	5	0·75	453	1	150–900	One tuft
	30	4·5	0·6	417	0·9	150–750	
H. firmus var. *longipes*	130	5	2·5	407	0·9	150–800	One tuft
	155	7	2·9	470	1	120–1340	
H. hypohaemactus	37	3	0·7	430	0·9	100–1000	One tuft
	35	3	0·7	515	1·1	100–1300	
	25	2·5	0·5	435	0·9	100–1050	
	20	2	0·4	400	0·9	175–850	

The gill arrangement

Since the gills subsequent to the primaries are regularly intercalated at the margin of the limb as the pre-existing gills diverge and before the inflation of the medulla, the number of gill ranks roughly measures the extent of marginal growth; other things being equal, the greater the extent of marginal growth the more the gill ranks, while the amount of inflation is secondary and immaterial to the origin of the gills. Analysis of the gill arrangement provides a convenient check on the direct analysis of the size of the fruit body. The data obtained from about eighty fruit bodies are enumerated in Table B.

The table shows two facts. Firstly, in those varieties with small fruit bodies, namely *sericeus*, *minimus* and *gracillimus*, the small size of the pileus is due to the lesser growth of the limb. This is the explanation deduced in the previous section for the shortness of the stem in var. *gracillimus*, and one is therefore justified in considering the fruit bodies of these varieties as juvenescent. Secondly, the variation in size of the fruit bodies growing in the same tuft is due partly to a lesser extent of apical growth and partly to the lesser inflation. When many primordia develop close together from the same my-

Table B. *Showing the relation between the gill arrangement and size of fruit body in* H. firmus

	Number of		Diameter in mm.		
	Primaries	Ranks	Pileus	Stem apex	
H. firmus var. *militaris*	30	2	42	12	One tuft
	31	2	37	10·5	
	29	2	33	9	
	32	1–2	29	6	
	30	2	27	9·5	
	32	2	27	7	
	30	2	22	5	
	30	1–2	19	5	
	29	1–2	18	5	
	31	1–2	15	5·5	
H. firmus var. *stratiotes*	25	2–3	30	8	One tuft
	21	2–3	30	7	
	19	2–3	28	7	
	15	2	18	2	One tuft
	12	1–2	14	1·5	
	11	1–2	12	1	
	36	3–4	40	11	One tuft
	35	3–4	40	11	
	34	3	39	9	
	33	3–4	38	9	
	32	3	36	7·5	
	33	2–3	25	4	
	35	2–3	18	3·5	
	34	2–3	12	2	
	28	2–3	20	4·5	One tuft
	25	2–3	20	4·5	
	23	2–3	20	4	
	28	2	14	3·5	
	24	2	14	3·5	
	34	3–4	31	5	Miscellaneous
	24	3–4	35	5·5	
	24	3–4	27	5·5	
	23	2–3	23	5	
	23	3–4	18	3·5	
	23	3	18	3·5	
H. firmus var. *flavus*	23	2	18	2	One tuft
	20	1–2	16	1·5	
	18	1–2	14	1·5	
H. firmus var. *flavo-albus*	25	3	25	6	One tuft
	21	2–3	20	4·5	
	19	2	18	4	
H. firmus var. *stenophyllus*	39	3	30	7	One tuft
	36	2–3	29	6·5	
	35	2–3	28	6	
	37	2	27	6	
H. firmus var. *longipes*	31	3	45	7	One tuft
	30	2–3	44	7	
	33	3	40	6·5	
	32	2–3	32	5·5	
	34	2–3	31	4·5	
	29	2	25	4	
H. firmus var. *sericeus*	12	1–2	10	1	One tuft
	12	1–2	9	1·5	
	13	1–2	7	1	
	13	1	6	1·5	
	14	1	5	1	
	12–18	1–2	5–12	1·5–2	One tuft
H. firmus var. *minimus*	7–10	1	4–10	0·5–1	One tuft
H. firmus var. *gracillimus*	10–12	1 (–2)	4–7	1	One tuft

celium, they grow equally for a short time, then some take the lead, developing normally, and the rest are more or less stunted: in fact, in caespitose species one can generally find in the mature tufts all transitions from fully developed fruit bodies to rudimentary and distorted primordia, and care must be taken not to include these abortive fruit bodies in material for developmental studies. Sometimes the stunted primordia have undergone their full amount of apical growth, for they possess the full complement of primaries and

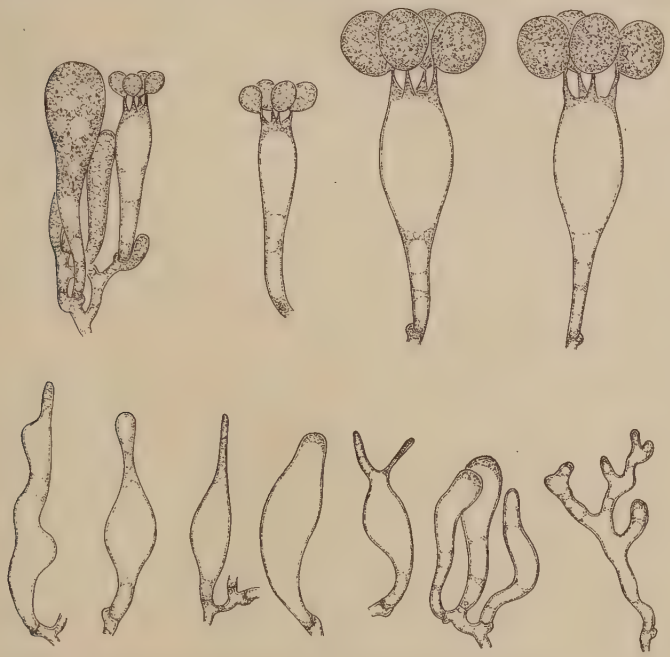


Fig. 6. Large and small basidia and cheilocystidia of *H. hypohaemactus*; × 1000.

gill ranks, but they are stunted through lack of water for inflation. Apical growth of other primordia may be checked prematurely and these develop into fruit bodies which are not merely small but which have fewer primaries and gill ranks. The mycelium lays down more initials than it can mature; their demands exceed the supply of food and water, and but a few develop normally. It is not until one begins to watch the primordia in the field that one realises how many failures there are. I have never seen an aborted primordial shaft expanded into a *Clavaria*-like body; unless the pileus is developed to an appreciable extent, the primordium aborts completely.

Discussion on development

Some American investigators have contended that the gills of agarics arise through the buckling of the hymenium as it undergoes intercalary growth and not by an active outgrowth along certain paths (2). They state that the hymenium of the primordium is at first flat and, as the basidia inflate and as more are intercalated sympodially, so the hymenium is compressed between the incurved margin of the limb and the stem apex: a tension develops which is relieved by throwing the hymenium into radial folds. That this explanation rests on misunderstanding is evident from the following considerations:

(1) It is not obvious that such a state of tension would be relieved by simple radial buckling. Considering the intricate connections of the hymenium it would most probably be thrown into anastomosing wrinkles, defining more or less hexagonal areas, *e.g.* the species of *Cantharellus*, *Craterellus*, *Cyphella*, *Marasmius*, *Campanella* and *Stereum* with wrinkled hymenium.

(2) Why should not such a lateral pressure cause merely a hyponastic curvature of the limb, which is free to move in either direction? Actually the tension in the primordial hymenium, when the gills are developing, is never enough to overcome that of the pile on the pileus which forces the limb towards the stem.

(3) If the gill ridges buckle out from the limb, why are there not schizogenous cavities overlaying the gills, like the hollow in the stem?

(4) Why are gill ridges not developed on the upper side of the pileus in species with a compact pile or palisade, *e.g.* species of *Boletus*, *Pluteus*, *Mycena*, *Marasmius*, *Psathyra*, *Coprinus*, etc.? Such a palisade of contiguous inflated cells, increasing their numbers by sympodial branching, presents exactly the same problem as the primordial hymenium. At most, anastomosing wrinkles develop, as in *Pluteus phlebophorus*, *Lactarius fuliginosus* and *Psathyra corrugis*.

(5) How can the secondaries and higher ranks be intercalated regularly by this means? When as rarely happens anastomosing wrinkles are developed, they offer no such order.

(6) How would the tramal hyphae stand the stretching? For the cells of some might be pulled out for several millimetres, and if they broke that part of the hymenium supplied by them would perish.

(7) Why should the tramal hyphae be so compactly arranged and strictly longitudinal in the typical gill?

I think that it will always be found that the gill ridges are lines of outgrowth as I have described in *Collybia apalosarca* and *Hygrophorus firmus*. But how they are blocked out at the margin of the limb by sectors of inhibition is a profound problem. The morphologist always comes against such barriers which limit his researches and show where he must hand over to the experimenter.

The biology of the fruit body

The fruiting of *Hygrophorus firmus* in Malaya is seasonal. It takes place during a week or two in each wet season after a dry spell, which must be of two or three weeks duration and pronounced enough to dry off the surface layer of humus in the forest. In Singapore such a spell generally occurs twice a year, in February and in July or August, and it is followed by a period of three to four months' intermittent rain during which the humus is always moist. The fruit bodies of *H. firmus* then begin to develop some six weeks after the break in the dry weather. Over a small area of forest where the rainfall is uniform, one may therefore find the troops of fruit bodies twice a year during one or two weeks, and only very sporadically, if at all, in the intervals. Each mycelium fruits once only in each season.

I have watched to completion the growth of forty-three fruit bodies of *H. firmus stratiotes*, and many others which were less complete.

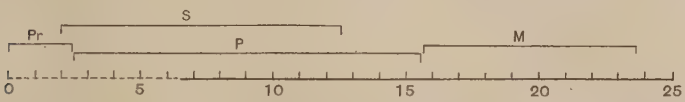


Fig. 7. A diagram of the life of a fruit body of *H. firmus* var. *stratiotes*: the continuous basal line covers the period of sporing: the figures are days (24 hours): *Pr*, the primordial shaft; *S*, stem elongation; *P*, pileus-enlargement; *M*, maturity.

Development is gradual. The total life of the fruit body varies from twenty to twenty-seven days, being generally twenty-three to twenty-four days. The apical growth of the primordial shaft occupies the first two or three days. The stem elongates during the next seven to twelve days; the pileus continues to expand for a further three to five days and the fruit bodies persist full-sized and mature for a final period of four to ten days. Sporing begins when the pileus is 4–6 mm. wide, that is to say on the sixth to seventh day. These facts are delineated for an average fruit body in Fig. 7. It is not, of course, easy to judge either when the primordium is initiated, because it is hidden in the soil, or when the fruit body is thoroughly effete, because the limb collapses gradually: a day or so may therefore be added or subtracted both from the beginning and the end of this scheme. But, certainly, the primordial shaft grows remarkably quickly. The stem elongates most rapidly during the interval from the seventh to tenth day, the pileus from the ninth to thirteenth day. The stem often begins to rot at the base before the limb collapses, especially if there is much rain, and this may cause the premature death of the fruit body.

The fruiting of *H. hypohaemactus* also appears to be seasonal, but

owing to its scarcity I cannot state this categorically. During the four years, 1929–32, it has fruited twice a year in the Singapore Botanic Gardens at intervals of two to four months after the break of the dry spell. It certainly develops much later in the wet season than *H. firmus*. General observations show clearly that the fruit bodies have a similar slow growth and long period of maturity, although I have not been able to study them in detail. This slow development and indefinite period of sporing is probably characteristic of the more massive gymnocarpic agarics such as *Hygrophorus*, *Clitocybe*, *Entoloma*, etc., and it is in striking contrast with the rapid evolution and precise mechanism of *Collybia apalosarca* and the angiocarpic genera *Amanita* or *Coprinus*.

Systematic section

Hygrophorus firmus B. & Br. (= *H. firmus* var. *typicus*).

Pileus 1–4 cm., at first convex, becoming plane and slightly umbilicate, sometimes infundibuliform or pervious to the base of the stem, *minutely scurfy squamulose over the disc*, innately fibrillose and striate toward the margin, *dry, orange-red or scarlet*, paler on expansion and pale yellowish when old; margin slightly incurved at first, often crenatoplicate.

Stem 3–8 cm. × 2–12 mm., equal, slightly thickened above or attenuate downward, dry, smooth, *becoming hollow*, rather stiff, often flattened below, *paler concolorous*, discolouring pale yellowish; base white, abrupt.

Gills shortly decurrent, often more or less broadly sinuate, *distant*, 1–4 ranks, with 16–40 primaries, 2–3·5 mm. broad, rarely forked near the stem, rather thick, not veined or very slightly, *concolorous at first, becoming pale yellow or whitish*, yellowish at the base; trama pallid yellowish.

Flesh thin, 1–2 mm. in the centre, 0·3–0·5 mm. half-way to the margin, watery, rather soft, *concolorous*; smell and taste none.

Spores white, ellipsoid, smooth, thin-walled, *dimorphous*: *large spores* 12–16 × 7–10 μ, broadly oblong ellipsoid, ends blunt, slightly flattened adaxially, sometimes narrowed distally rather suddenly and waisted, with a prominent lateral-basal apiculus, *with dense granular-oleaginous contents*: *small spores* 5–8 × 3·5–4·5 μ, more or less pip-shaped, widest in the proximal half, *with hyaline, cloudy vacuolate contents*.

Basidia dimorphous: *large basidia* 50–75 × 12–16 μ, clavate, with dense granular-oleaginous contents at first, becoming hyaline, with four large sterigmata 8–11 × 3–4 μ at the base: *small basidia* 28–40 × 6–8 μ, subclavate or subcylindric, contents cloudy-vacuolate, with four, rarely two, sterigmata 5–7 × 1·5–2 μ at the base.

Cheilocystidia 25–60 × 7–30 μ, cylindric, clavate or vesicular, rarely ventricose, thin-walled, colourless, vacuolate, sometimes with one to five short cylindric processes up to 5 μ long from the distal end, as abortive sterigmata: forming a narrow sterile edge, often inconspicuous and with all transitions to sterile basidia.

Caulocystidia absent or as a few irregular sterile basidia at the apex of the stem.

Habitat, in troops or small tufts in the lowland and mountain forest up to 4000 ft.; Ceylon, Malaya.

The varieties of *H. firmus* can be arranged in two sections, Ovalisporae and Macrosporae. I have given, in the following descriptions, only the distinctive characters of the varieties which in other respects, unmentioned, may be taken as identical with the typical state.

Ovalisporae. Sporis magnis 12–16 × 7–10 μ, late ellipsoideis vel ovoideis, apicibus obtusis, vix attenuatis.

var. ***militaris*** var.nov.

Stipite albo vel primo pallide flavo.

This variety appears commoner than the type, at least in Singapore. Growing in troops, with scarlet cap and stiff white stem, its carriage is soldierly.

var. ***puniceoides*** var.nov.

Pileo 7–8 cm. lato, magno, convexo-plano, non umbilicato: stipite 6–7·5 cm. × 7–9 mm., claro flavo: lamellis latis, 6–10 mm., adnexis, saepe dentibus parvis decurrentibus praeditis, pallide citrino-flavidis: carne crassa, 3–4 mm. medio pileo, pallide alba: sporis magnis minusculis, oblongis, saepe paulo constrictis, 12–15 × 7–9 μ.

I found this variety once, at Tembeling in Pahang, November 4th, 1930. Macroscopically it is so like *H. puniceus* that one would not consider it related to *H. firmus*, although microscopically it is essentially the same.

Macrosporae. Sporis magnis 16–25 × 7–11 μ, longo-ellipsoideis, plus minus fusiformis, saepe paulo curvatis vel allantoideis, apicibus subacutis, distincte attenuatis.

var. ***stratiotes*** var.nov.

Forma typica persimilis sed sporis majoribus, 18–25 × 7–11 μ.

Macroscopically this variety is indistinguishable from the typical state. The basidia are generally of the same size, though the large ones may reach 18 μ wide. It is the commonest variety in Malaya, and I have found it frequently in Singapore, Johore, Pahang and Negri Sembilan, where it may be expected every season.

var. ***pallidipes*** var.nov.

Stipite albo.

This variety stands to var. *stratiotes* as var. *militaris* to the typical state. It is not uncommon.

var. ***depallens*** var.nov.

Pileo albido vel flavido, raro carneo-flavido: stipite 7–10 cm. × 4–6 mm., flavido, apice albo, vel ex integro albo: lamellis latis, 6–7 mm., pallide carneo-ochraceis.

I have found this variety only in the Reservoir Jungle in Singapore. It is poorly pigmented and the pinkish gills suggest *Entoloma* or *Leptonia*.

var. ***sericeus*** var.nov.

Pileo parvo, 5–12 mm., cano-albo, subfibrilloso, sicco atomato, stipite 2–2·5 cm. × 1·5–2 mm., ceraceo, citrino-flavido: lamellis albis dein pallide carneis: sporis magnis 16–21 × 6·5–9 μ: sporis parvis 6–8·5 × 3–3·5 μ.

I have found this variety on the hill, Bukit Timah, in Singapore. Macroscopically it exactly recalls *Leptonia sericella*: the loose, sparingly branched, decumbent hyphae give the limb the silky fibrillose appearance. It differs from var. *depallens* in the smaller size, narrow gills, smaller spores and paler colour.

var. ***flavus*** var.nov.

Stipite et pileo citrino-flavo vel saturatiori: lamellis flavidis, dein albidis: sporis magnis 16–22 × 10–11 μ: sporis parvis 5–7 × 3·5–4·5 μ.

This variety appears every year in the Aroid Rockery in the Singapore Botanic Gardens, where there are many forest trees. The fruit body is brilliant yellow without a trace of red.

var. ***flavo-albus*** var.nov.

Pileo flavido: stipite albo: lamellis albis, latis, 4–6 mm.

This variety is so very close to the preceding that, perhaps, it hardly deserves a name. It is a further step, however, to the following albino condition. I have found it in the Reservoir Jungle, Singapore. Bresadola's illustration of *H. lucorum* (*Iconogr. Mycol.* VII, 314) would pass macroscopically for this variety.

var. ***albus*** var.nov.

Ex integro albus.

I found a troop of fourteen fruit bodies of this variety by the Cheka River in Pahang, on November 12th, 1930. The fruit body is devoid of pigment, though in shape, size, and microscopic characters identical with var. *stratiotes*.

var. ***roseus*** var.nov.

Pileo purpureo-roseo vel carneo: stipite albo vel pallide carneo: lamellis pallide carneis, pallescentibus.

This variety is not uncommon. I have found it in Singapore and at Tembeling and Fraser's Hill (4000 ft.) in Pahang. The fruit bodies are often rather larger than typical, especially in length of stem. It leads both to the following and to var. *longipes*.

var. ***amethystinus*** var.nov.

Pileo purpureo-vinaceo: stipite albido: lamellis claro amethystinis, ut *Laccaria laccata* var. *amethystina*.

I found this most striking variety as a troop of twenty fruit bodies in the forest at Tembeling, Pahang, on November 9th, 1930. The

colour is so unlike that of a *Hygrophorus*, lacking all trace of red and yellow, that it suggested *Tricholoma* or *Clitocybe*. Microscopically it is indistinguishable from var. *stratiotes*.

var. ***pachyphyllus*** var.nov.

Pileo 5–6 cm. lato: lamellis perlatis, crassis, 8–10·5 mm. latis, ad basim 2 mm. crassis.

I have not analysed the property of thick gills in this variety, but it is doubtless caused both by an excessive marginal growth and inflation or intercalary growth. It occurs not infrequently in the Reservoir Jungle, Singapore.

var. ***stenophyllus*** var.nov.

Pileo convexo-plano, citrino-flavo: stipite citrino-flavo: lamellis albis, angustis, 2–2·5 mm. latis, subdecurrentibus, late sinuatis vel subarcuatis.

I found a troop of some fifty fruit bodies of this variety on Fraser's Hill, Pahang, May 27th, 1930, at 4000 ft. altitude. Only the largest fruit bodies had spores; those with pilei less than 16–20 mm. wide were not yet fertile. It may be an abnormal form of var. *flavus*, partly sterile and thus with narrow gills.

var. ***longipes*** var.nov.

Stipite saepe altissimo, 5–17 cm., apice 4–7 mm., basi 5–10 mm., albo: lamellis saepe perdecurrentibus, 3·5–4·5 mm. latis, albis.

The pileus is typical, 2·5–4·5 cm. wide, scarlet fading to orange or pale yellow, and with the full gill complement. The enormous length of stem, as shown in the preceding section, must be due to long-continued apical growth of the primordial shaft, since the average inflation of the cells is typical. Such a state might be evoked through an external factor as weak light, unusual temperature or high humidity, but the fruit bodies may be found in open sunny places by paths in the forest, in deep shade, in humus, or on bare sandy banks, and both in the lowlands and the mountains. I have found it at Padang Piol, near Tembeling, and at Fraser's Hill (4000 ft.) in Pahang. In the collection from Padang Piol and most of those from Fraser's Hill the spores are as in var. *stratiotes*, but in one collection from Fraser's Hill they were unusually large, as shown in Fig. 8 *e*: the large spores measured 22–27 × 9–11 μ and the small spores 9–12 × 4–4·5 μ. Scattered through the forest on Fraser's Hill I have also seen specimens of this variety which were wholly white or with the faintest tinge of yellow on the pileus, but I have no accurate data on them.

var. ***minimus*** var.nov.

Pileo pusillo, 4–10 mm. lato, convexo-plano, raro subumbonato vel subum-

bilicato: stipite brevissimo, 5–10 × 1 mm., solido: lamellis arcuatis, perdecurrentibus, distantis, 7–10 primis, ordine uno, raro secundo incompleto, instructis.

Apart from their minute size, the fruit bodies of this variety are identical with those of var. *stratiotes*. As shown already, they must be regarded as juvenile forms with limited apical growth and normal turgescence. It is not infrequent, but easily overlooked. I have found it in Singapore, round Gunong Panti in Johore, and at Tembeling in Pahang. Generally the fruit bodies are scattered and few.

var. ***gracillimus*** var.nov.

Pileo pusillo, 4–7 mm. lato, convexo-plano, subumbonato, plus minus turbinato, flavido vel albido, centro saturatiori carneo-aurantiaco: stipite gracili, 15–25 × 1 mm., solido, translucido, pallide aurantiaco: lamellis subtriangulis, breviter decurrentibus, uno ordine, raro secundo incompleto, instructis, 10–12 primis, 1–1·5 mm. latis: sporis 18–23 × 9–10, et 8–10 × 3·5–4 μ.

This variety differs from the preceding in the longer, slender stem and pale colour. It looks like an *Omphalia*. I have found it only on Fraser's Hill by the path to the waterfall, but in a troop of over a hundred individuals growing in moss on a sandy bank, and in two successive seasons, in May and November, 1930.

Hygrophorus hypohaemactus spec.nov.

Pileus 2–2·7 cm. latus, convexus dein planus, margine primo incurvato, *viscoso-papillosus*, *glutine hyalino* griseo viscido adnato, in medio pileo 1–1·5 mm. crasso, marginem versus tenuiori, saepe supra marginem in vittas triangulas usque 1 mm. longas projicienti, *obtectus*, *umido striatus*, sub glutine *rubro-sanguineus*, *dein pallescens*, demum pallide aurantiacus vel flavidus.

Stipes 3–6 cm. × 2·5–3·5 mm., *cylindricus*, solidus dein cavus, *viscidus*, glutine simili, saepe peronato-disrupto vel crispato, obtectus, *pallide aurantiacus vel rubro-aurantiacus*, demum pallescens.

Lamellae adnatae vel adnexae, separantes, *subdistantes*, crassiusculae, ordinibus 3–4 instructae, primae 18–20, 2·5–3·5 mm. latae, *ceraceo-submucosae*, margine obtuso continuo dein mucoso et interrupto praeditae, *albae*, *basim versus pallide aurantiacae*.

Caro tenuis, medio pileo 1–1·5 mm. crasso (glutine subtracto), *concolor*: odore deficiens.

Sporae albae, laeves, dimorphae: *sporae magnae* 8–10 × 6·5–8·5 μ ovoideae vel lato-ellipsoideae, intus granuloso-oleaginosae: *sporae parvae* 4–5 × 3–3·5 μ, subglobosae, basim versus attenuatae, intus nebuloso-vacuolatae, vix vel haud granulosae.

Basidia dimorpha: *b. magna* 33–44 × 10–12 μ, stipitato-ventricosa sterigmatis 4, 5 μ longis, praedita: *b. parva* 20–28 × 5–6 μ, subclavata, sterigmatis 4, 3–3·5 μ longis, praedita.

Cheilocystidia 16–40 × 4–9 μ, polymorpha, subclavata, clavata, ventricosa, saepe flexuosa, hyalina, vacuolata, tenuiter tunicata, apicibus plerumque simplicibus, saepe 1-ramosis vel lobatis vel appendicibus 2 sterigmatoideis praeditis: *pleurocystidia* vera absentia.

Hab. ad terram in silvis: Malaya.

I have found this species only in the Garden's jungle and once at Tembeling, in Pahang. It has caulocystidia only at the extreme apex of the stem where they are like the cheilocystidia but rather longer,

up to 60 μ, more flexuous and more branched and irregular, and they form a few compact clusters, as in *H. firmus*, immediately preceding the hymenium.

Systematic discussion

It is not easy to decide in a species so variable as *Hygrophorus firmus* which state shall be reckoned the typical. Very fortunately the collections from Ceylon, whence the species has hitherto been known, are the most generalised and approach nearest to what is supposedly the ancestral state. They are thus qualified on grounds other than mere "type collection" to hold such a position. The same state occurs in Malaya, and with the local material I have amplified Petch's description in the foregoing section as *H. firmus* var. *typicus*. These dimorphous species are surely derived from the section of *Hygrophorus* including *H. miniatus*, *H. Reai*, *H. turundus*, etc., which have fruit bodies of similar shape, colour and manner of development. The spores of this section are typically subglobose, 6–9 × 4–7 μ, with fairly dense, granular or cloudy vitreous contents, and not only do the large spores of *H. firmus* pass through such a stage in their development but those of *H. hypohaemactus* are little removed from it and lead through the Ovalisporae to the Macrosporae (*vide* Fig. 8). The fruit bodies of this section are also of medium size and more or less fully pigmented as in *H. firmus* var. *typicus*. Thus the other states of *H. firmus* may be looked upon simply as variants in size and pigmentation. Regarding these varieties there are the following facts:

(1) In any one troop the fruit bodies, which are presumably derived from the same mycelium, all have the same special characters. I have never seen two varieties mixed in the same troop or even growing in the immediate vicinity of each other.

(2) The same varieties occur in such widely separate localities as Singapore, Johore and Pahang, *e.g. stratiotes*, *militaris*, *minimus*, *pallidipes*, *roseus* and *longipes*.

(3) Certain varieties I have found repeatedly on the same patch of ground each season so that their mycelia must have constant characters, *e.g. militaris*, *stratiotes* and *flavus* in the Singapore Botanic Gardens (1929–32), *pallidipes* in the Reservoir Jungle, Singapore (1930–32), and *gracillimus* and *longipes* on Fraser's Hill, Pahang (May, November, 1930).

The characters of the varieties are clearly fixed and hereditary, and it is a problem whether some should not rank as species. Indeed, should not one propose a new genus based on the dimorphous spores, with two subgenera, the one for *H. firmus* with dry pileus and stem and the other for *H. hypohaemactus* with viscid? Yet it is equally clear that many of the varieties are merely colour forms and that intermediates will probably be found. Moreover, anatomical knowledge

of the Hygrophorei is far too meagre to allow the recognition of natural genera. Is it usual in *Hygrophorus* for some only of the hyphae to inflate the fruit body? I would have refrained even from varietal names were they not necessary for accurate description and to emphasise the extraordinary range in size, shape and colour which *H. firmus* displays. And though it is a common species, many years must elapse before we have a full knowledge of it: the period of fruiting is so brief that one traverses the forest without meeting with it many times. The following remarks therefore are only tentative.

The Ovalisporae may differ specifically from the Macrosporae. The spores of *H. firmus* are fusiform-ellipsoid because the stiffening of the distal part of the wall, when the spore is in the subglobose

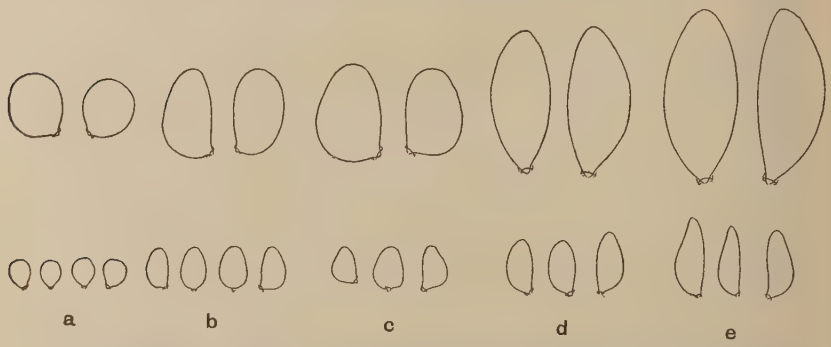


Fig. 8. Large and small spores: *a*, *H. hypohaemactus*; *b*, *H. firmus* var. *puniceoides*; *c*, *H. firmus* var. *typicus*; *d*, *H. firmus* var. *stratiotes*; *e*, *H. firmus* var. *longipes* (Fraser's Hill, *vide* text); × 1000.

stage, is delayed and this part is further protruded into a subacute apex through the pressure in the basidium, and the process is carried farthest in the Macrosporae. In the Ovalisporae, var. *puniceoides* might be separated specifically from *H. firmus* var. *typicus* and var. *militaris* on the shape and colour of the fruit body and the rather smaller spores, which are most like those of *H. hypohaemactus*. In the Macrosporae, probably only var. *gracillimus* deserves specific rank. The varieties *longipes*, *minimus* and *pachyphyllus* are only growth forms. The remainder are chiefly colour forms in which the pigment is either limited to certain parts or modified into yellow, pink or purple. The varieties *stenophyllus* and *sericeus* combine differences both in colour and form.

H. similis Petch is macroscopically very like *H. firmus*, but its spores are monomorphous and narrowly ellipsoid or subcylindric, 6–9 × 3–3·5 (–4) μ. I have examined part of the type collection, Herb.

Perad. 5580. It seems very close to *H. Reai*, but I could make out no structural details in the dried specimen.

Finally it must be remarked that Petch's statement that the large spores of *H. firmus* are verrucose is an error. I have examined Herb. Perad. 2299, determined by Petch, and find the spores smooth. It is well known that a densely granular cytoplasm may give the appearance of a rough epispore when the spore wall is very thin and transparent, and an immersion lens is needed to decide the point.

Summary

Hygrophorus firmus and *H. hypohaemactus* sp.nov. form two kinds of basidiospore. In the same fruit body they produce large spores with dense contents on large basidia, and small spores of half the linear measure and with vacuolate contents on small basidia. The meaning of the dimorphism is unknown.

Both species occur in Malaya, *H. firmus* being known previously from Ceylon. *H. firmus* in Malaya is exceedingly variable. Sixteen varieties are proposed under two sections according to the spore character: most are colour varieties but some are shown to be juvenile forms, others to be overgrowths. *H. hypohaemactus* is rare.

H. hypohaemactus differs from *H. firmus* in the viscid pileus and stem and in the smaller less dimorphous spores. Both are related to the group of *H. miniatus*, *H. turundus*, etc. The systematic position is discussed.

The structure, development and variation in size of the fruit body are explained in detail.

The fruit body of *H. firmus* is gymnocarpic with exogenous pileus. There is a pile on the pileus, at least over the disc, but not on the stem. The gill edge is sterile with cheilocystidia: there are no pleurocystidia. Development is gradual, occupying about a fortnight. The growth of the primordial shaft takes two to three days. The stem and pileus slowly inflate acropetally during the next ten to twelve days. The mature fruit body lasts about a week, making the total life a little more than three weeks. Sporing begins about the sixth day when the pileus is 4–6 mm. wide. These observations were made in Singapore at a mean temperature of 80° F. (70–90° F.).

The limb and gills develop by apical growth of the hyphae followed by acropetal inflation, exactly as the primordial shaft. In the stem and pileus many hyphae do not inflate but are passively drawn out. Both kinds of basidium are borne on the same hyphae, the large basidia being the first formed and arising deeply in the subhymenium. The large spores are carried beyond the level of the small spores. The hymenium is aequihymeniiferous.

The fruit body of *H. hypohaemactus* is essentially similar, but the

hyphae of the pile on the pileus and those on the surface of the stem and in the subhymenium have mucilaginous walls, and there are peculiar hypha-like tramal cystidia with oleaginous contents in the gills.

I must, in conclusion, express my obligation to the Director of Agriculture, Ceylon, for the loan of authentic material and drawings of the several species of *Hygrophorus*.

REFERENCES

(1) Buller, A. H. R. *Researches on Fungi* (1922, 1924).
(2) Corner, E. J. H. "An evolutionary study in Agarics: *Collybia apalosarca* and the veils." *Trans. Brit. mycol. Soc.* xix (1934).
(3) —— "Studies in the morphology of Discomycetes." *Trans. Brit. mycol. Soc.* xiv (1929).
(4) Petch, T. "Revisions of Ceylon Fungi. Pt. V." *Ann. R. bot. Gdns Peradeniya*, vi (1917), 323.

Fig. 1.

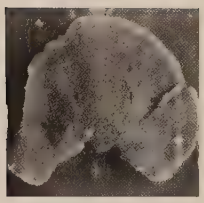


Fig. 2.

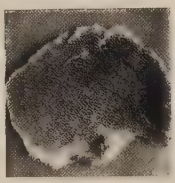


Fig. 3.

Fig. 4.

Polystictus xanthopus

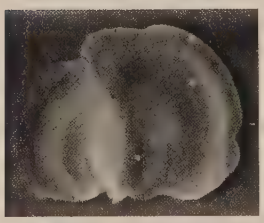


Fig. 5.

Fig. 6.

Polystictus flabelliformis

A NOTE ON THE VARIATION OF PORES OF *POLYSTICTUS XANTHOPUS* FRIES AND *POLYSTICTUS FLABELLIFORMIS* KL. AT HIGH ALTITUDES

By S. R. BOSE

Professor of Botany, Carmichael Medical College, Calcutta, India

(With Plate II)

The hymenial surface of specimens of *Polystictus xanthopus* Fr. at high altitudes shows three different kinds of porous areas, viz. some with typical very small pores, some with much bigger pores and some with hydnoid pores (Pl. II, figs. 1, 2 and 3). In one piece of dead branch of a tree, specimens with typical pores and hydnoid pores were growing not very far off from each other (Pl. II, fig. 4), and so it is concluded that they are variations of one and the same species. Such variations are hardly found in the plains where the fungus is abundant, with very small typical pores on the hymenial surface.

Specimens of *P. flabelliformis* Kl. similarly collected from high altitudes show two kinds of porous surface, some with very small pores and others with much bigger pores (Pl. II, figs. 5 and 6). In other respects, morphological and anatomical, the specimens are exactly similar. In the plains we always get them with small pores on the hymenial surface.

This illustrates, as has been noted by French mycologists (Sauger, Josserand, Maire, etc.), that the dimension of the pores in the hymenial surface—one particular character—is not always a safe guide in the delimitation of species.

The specimens described in this note were collected from high hills of four different localities: (1) Cherrapunji, Assam, by me (8000 ft. elevation) in March, 1929; (2) Lokra hills (8000–10,000 ft. elevation) by Dr N. L. Bor in January, 1934; (3) Bhutan border (10,000 ft. elevation) by Mr K. P. Biswas, Curator of the Shibpur Herbarium Royal Botanic Gardens, in April 1934; (4) Pareshnath hills (2000 ft.) by Mr K. P. Biswas in November 1934.

NOTE ON ABNORMAL SPORES IN *PODOSPORA MINUTA*

By WINIFRED M. PAGE, M.Sc.

(With 5 Text-figures)

Podospora minuta occurs commonly on rabbit pellets. It appears early in the succession of fungi, usually fruiting at the same time as *Ascophanus carneus* and other Discomycetes.

The spores germinate readily and single-spore cultures are easily obtained.

Fig. 1. Types of asci showing variation in number of spores and abnormal spores. × 200.

The normal asci contain four spores, each of which is capable of producing a mycelium giving rise to fruits (Fig. 1 *f*). In perithecia grown in culture and also in those growing on rabbit pellets collected

from various sources, asci with abnormal spores sometimes occur. From one to seven spores which, apart from size, are normal in appearance have been observed (Fig. 1 *a–i*). In addition irregular spores, some of which never completely darken, are occasionally

	1	3	4	5	2	6	7
1					●	●	●
3					●	●	●
4					●	●	●
5					●	●	●
2	●	●	●	●			
6	●	●	●	●			
7	●	●	●	●			

Fig. 2. Table showing results of crossing mycelia from A and B spores.

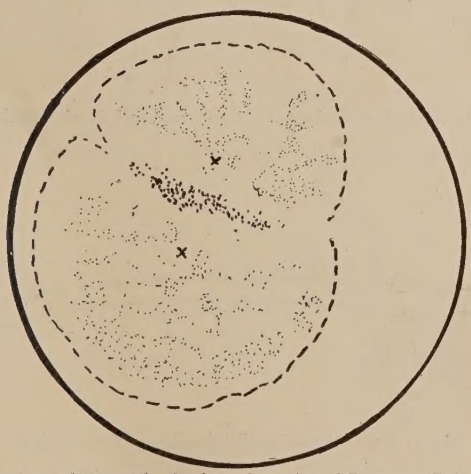


Fig. 3. Diagram from photograph of culture from A and B spores. Points of inoculation indicated by ×. The fine dots show abortive perithecia and the broken lines the limits of the mycelia.

seen (Fig. 1 *j–m*). Of asci with other than four spores, the one giant and two normal is the most common variety (Fig. 1 *c–e*). Asci with two dwarf and three normal spores are not so frequent, but a number of the dwarf spores have been isolated and germinated (Fig. 1 *g*). As in *Sordaria fimicola* (four-spored form) the perithecium initials in

the mycelia from these spores never mature. When the spherical stage is reached no further development takes place (4, 5, 6).

The mycelia from these dwarf spores were found to be of two different, but complementary, strains. A number of crosses were

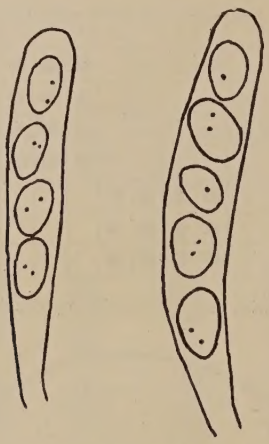


Fig. 4. Sections of young four- and five-spored asci showing nuclei. × 400.

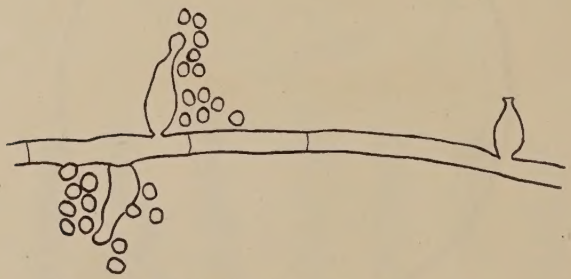


Fig. 5. Formation of small colourless spores. × 1600.

made and the results are shown in the table (Fig. 2). The details of the results agree with those of *Sordaria fimicola* (6).

The normal spores contain two nuclei and the dwarf spores one nucleus each (Fig. 4).

The eight-spored form of this fungus is not common; I have found it only once in many years of collecting. It was, however, cultured. Each of the eight spores is uninucleate and capable of producing mycelia which fruit.

In the four-spored variety very tiny colourless spores are produced, being cut off from flask-shaped outgrowths (Fig. 5). These have been seen in normal cultures and also in those from dwarf spores. Work on these spores is now in progress, and up to the present there has been no indication that they possess the functions predicated for the "micro-conidia" by Ames in *Podospora* (*Pleurage*) *anserina*(1, 2, 3). The perithecium initials, whether normal or abortive, early send out branches to form secondary mycelia, but there is no evidence that any of these can be described as a trichogyne.

It is interesting to note that Winter in 1873 figured an ascus with two spores in *Sordaria* (*Podospora*) *anserina*(7).

REFERENCES

(1) Ames, L. M. "A study of some homothallic and heterothallic Ascomycetes." *Mycologia*, xx (1930), 318.
(2) —— "An hermaphroditic self-sterile but cross-fertile condition in *Pleurage anserina*." *Bull. Torrey bot. Cl.* lix (1932), 341.
(3) —— "Hermaphroditism involving self-sterility and cross-fertility in the Ascomycete *Pleurage anserina*." *Mycologia*, xxvi (1934), 5.
(4) Dowding, E. Silver. "The sexuality of the normal, giant, and dwarf spores of *Pleurage anserina* (Ces.) Kunze." *Ann. Bot.* xlv (1931), 1.
(5) —— "Gelasinospora, a new genus of Pyrenomycetes with pitted spores." *Canad. J. Res.* ix (1933), 294.
(6) Page, W. M. "A contribution to the life history of *Sordaria fimicola* (four-spored form) with special reference to the abnormal spores." *Trans. Brit. mycol. Soc.* xvii (1932), 296.
(7) Winter, G. "Die deutschen Sordarien." *Abh. naturf. Ges. Halle*, xiii (1873).

A SIMPLE METHOD OF PRESERVING AND MOUNTING SPECIMENS OF FUNGAL LESIONS ETC. FOR DEMONSTRATION

By N. C. PRESTON

When engaged on infection experiments with *Myrothecium roridum* I had need of specimens of the lesions produced on stem and leaves which would remain fresh and demonstrable over a considerable period and which could be easily transported. The procedure here described was therefore adopted with considerable success and, since it is extremely simple and is very rapidly carried out, it is thought that this brief description will be of interest to other workers.

A 2 per cent. solution of agar containing about 0·1 per cent. mercuric chloride is prepared and poured into Petri dishes of suitable size. When this has cooled to near solidifying point the leaves or other pieces of tissue are plunged, without previous preparation, directly into the agar and held beneath the surface with a warm needle until the mass has solidified sufficiently to retain them in position. The depth of agar in the dish will of course depend upon the thickness of the object to be embedded and should be just sufficient to cover it evenly. The agar must not be used too hot or the colour of the material will be lost.

Specimens prepared in this way will keep for many months, retaining their natural appearance even after the agar has become dry and hard. The method of mounting also has the advantage that both sides of the object can be closely examined since the lid of the dish may be safely removed without fear of mould contaminations. In specimens kept unsealed for six months hyphae and spores of the sporodochia present upon the leaves were still easily visible under a $\frac{1}{6}$ in. objective.